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# A COMBINED CLADISTIC ANALYSIS OF ANGIOSPERMS USING *rbcL* AND NON-MOLECULAR DATA SETS<sup>1</sup>

Owi I. Nandi<sup>2</sup>, Mark W. Chase<sup>3</sup> and  
Peter K. Endress<sup>2</sup>

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## ABSTRACT

A combined analysis of 162 extant angiosperm taxa for which *rbcL* sequence-data and/or an appreciable amount of non-molecular information is available was calculated. A non-molecular tree, an *rbcL* tree, and a combined tree are presented. Only the *rbcL* and the combined data set show large numbers of groupings with bootstrap percentages greater than 50%, whereas the non-molecular trees show only eleven clades of this kind; this seems due to the number of missing cells in the non-molecular matrix. We tried to identify non-molecular characters (including biochemical) that support groups present in these analyses, especially in cases where clades turned out to be new when compared to one or more "classical" taxonomic systems. New groupings found in the non-molecular analysis that parallel the *rbcL* topologies include a grade containing Illiciales, Austrobaileyaceae, and Amborellaceae (magnoliid II); a clade containing Magnoliales, Laurales, Aristolochianae, and monocots (magnoliid I); a hamamelid group; subgroups of asterids (e.g., a similar asterid III clade containing Scytopetalaceae, Lecythidaceae, Sapotaceae, Ebenaceae, Theaceae, Primulales, Styracaceae, Marcgraviaceae, Actinidiaceae, Clethraceae, and Ericales); an expanded Caryophyllid group; a Malvales s.l. clade; a partial Malpighiales grade containing Quinaceae, Linales s. str., Passiflorales, Violaceae, Kiggelariaceae, Flacourtiaceae s. str., and Ochnaceae; and some smaller clades, similar to the corresponding groups found in *rbcL* cladograms (Illiciales–Austrobaileyaceae; Aristolochianae–monocots; Hydrangeaceae–Cornales; Lecythidaceae–Scytopetalaceae; Pittosporaceae–Araliales; Geissolomataceae–Stachyuraceae; Connaraceae–Oxalidaceae). Capparales s.l. and the nitrogen-fixing clade, two novel molecular clades, are only found in the *rbcL* and the combined trees. Cistaceae have been shown to share important characters with Malvales s.l. and are consistently found within this clade. These findings argue against their previous inclusion in Violales. The *rbcL* tree contains 38 terminal taxa that are included for the first time in a published phylogeny. Considerable progress has been made in assembling a morphological/chemical data set that parallels the broad coverage of angiosperms seen in DNA studies.

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New opportunities for the study of seed-plant phylogeny have opened due to the continued development of computer hardware and software. In addition, gene sequencing has become reasonably fast, and large nucleotide data matrices have been produced (e.g., Chase et al., 1993; Savolainen et al., 1996; Soltis et al., 1997b). These studies have stimulated even more molecular work on macrosystematics, including the addition of more "critical" taxa to the data matrices, comparison with results from other gene sequences, and the combination of nucleotide with non-molecular data matrices, as has been undertaken in this study. Other examples of broadly sampled combined nucleotide and non-

molecular studies are those of Doyle et al. (1994) and Chase et al. (1995).

The non-molecular investigations of this study originated from the question of the position of Cistaceae within eudicots. Cistaceae have been included in Violales (Takhtajan, 1966; Cronquist, 1981) and Malvales (Dahlgren, 1980), yet the most natural (i.e., phylogenetic) position has remained a matter of debate (Thorne, 1983, 1992). Thus, it was a major objective of our non-molecular study to identify the accurate position of Cistaceae and their allies (Bixaceae and Cochlospermaceae) within the eudicots. Most families that have commonly been allied with Malvales or Violales are included in

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<sup>2</sup> Institute of Systematic Botany, University of Zürich, Zollikerstrasse 107, 8008 Zürich, Switzerland.

<sup>3</sup> Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3DS, United Kingdom.

the present study. Many more taxa were added to evaluate the robustness and position of the two orders within eudicots and to compare the trees obtained with other studies (Hufford, 1992; Olmstead et al., 1992; Albert et al., 1992; Chase et al., 1993).

Monophyly of the taxa used has also been evaluated by comparing molecular results with macro-systematic studies (e.g., Urticales: Berg, 1977). This was done to determine which terminal taxa should be used in the non-molecular sampling. In the non-molecular matrix we make use of those clades found in the *rbcL* analysis that are compatible with widely accepted groups. Thus in some cases we have sampled individual families, whereas in others we have used orders (e.g., Gentianales, Annonales, etc.), superorders (e.g., Faganae, Aristolochianae), or larger groups (e.g., monocotyledons) that no recent research (molecular or non-molecular) has indicated are other than monophyletic. Flacourtiaceae s.l. were split into two groups, one with cyanogenic glycosides (e.g., Kiggelariaceae) and one without.

A major caveat for the non-molecular matrix is that we often used single character-states for polymorphic taxa. These assignments are based on assumptions of character polarity, which could result in mistaken interpretations of character evolution. We accept that in some specific cases mistakes may have been made, but we felt that some simplifications were required to deal with such large taxonomic units. However, the character-state assignments were carried out using a consistent approach (see Appendix 5). Because the independent trees are often highly similar, we gain confidence that the historical signal present in the non-molecular data has not been grossly distorted by this method of character-state assignment. We hope that further progress in non-molecular investigations will obviate the need for such a procedure in future studies. We are certain that this approach can be greatly improved upon. Analysis of large, non-molecular matrices is not without precedent in plant systematics (e.g., Donoghue & Doyle, 1989). Working with such large non-molecular matrices could have undesirable effects (i.e., not finding the shortest trees or all islands of trees, cf. Maddison, 1991). These large matrices must nonetheless be much less confounding than matrices using exemplar taxa for groups that are not monophyletic.

We were interested in finding a large set of non-molecular characters that would contain phylogenetic information. We tried to characterize larger taxonomic groupings, especially new ones, by non-molecular synapomorphies, as produced by MacClade 3.04 (cf. Maddison & Maddison, 1992). We

wanted to see in which way the non-molecular data set changed or confirmed the topology of the *rbcL* tree, and vice versa, when both data sets are combined (we agree that the inclusion of *rbcL* results in delimiting the terminal taxa and in looking for taxa with more ancestral characters within the larger of these terminal taxa makes it impossible to claim that both data sets are totally independent). We also examined by simple comparison whether the different samplings of taxa in the *rbcL* analysis of Chase et al. (1993) and that of the present study affect the topology of the *rbcL* tree. Finally, we were also interested in the stability of the topologies obtained after applying the parsimony jackknife program (Farris et al., 1997) and bootstrapping (Felsenstein, 1985).

## MATERIAL AND METHODS

### GENERAL METHODS

The matrices were analyzed using PAUP 3.1.1 (Swofford, 1993). The shortest trees were collected and swapped on to completion, keeping in this case all additional trees found at this shortest branch length. In the Results and Discussion sections, we will mostly use the same terms for the larger angiosperm clades used by Chase et al. (1993: part B of figs. 1–15) to facilitate comparisons.

*Ceratophyllum* was specified as the outgroup in agreement with the results produced with *rbcL* (Chase et al., 1993). We simply used *Ceratophyllum* as the outgroup to avoid the issue of where in the angiosperms the root should be placed. This topic will be discussed in other papers; we view it as too complex an issue to be dealt with adequately here. The use of non-angiosperm outgroups (Gnetales) for the non-molecular matrix is difficult. Important morphological structures cannot be adequately addressed in terms of their homology at present. Because we used *Ceratophyllum* as the default outgroup, we will not concern ourselves with the evaluation of its position. We were interested only in examining general patterns within the angiosperms for both *rbcL* and non-molecular data. All matrices are available on diskette or by e-mail (m.chase@rbgkew.org.uk) from the second author (please provide a single high-density diskette).

In each case, the products of the initial searches were sets of trees with equally weighted characters.

We intended to use the jackknife procedure of Farris et al. (1997) but found that the number of missing cells in these matrices makes this method unsuitable because it found no support for any groupings in the combined matrices [J. Farris, pers. comm., reports that missing data significantly lower

jackknife values; we have also investigated this empirically in another study (Fay et al., 1997). We therefore used the bootstrap consistently for an easier comparison. For trees illustrated in this paper, branch lengths are shown above the branches (ACCTRAN optimization, Swofford, 1993), and all branches not present in the strict consensus trees are indicated by an arrow. Bootstrap support for supported groups is indicated below the branches.

#### NON-MOLECULAR DATA MATRIX (APPENDIX 1)

A selection of 161 angiosperm taxa was scored for 252 characters (Appendix 3); 151 taxa were ultimately included in the non-molecular search (115 families, 32 orders, and 4 supraordinal taxa, mainly in the sense of Takhtajan, 1987; Appendix 2). Data were taken from selected synoptic literature, from primary literature (especially in dilleniids sensu Cronquist, 1981) and from original observations by the first author [leaf venation and dentation (studied in the Herbaria of Zürich, Geneva, and Vienna and in a number of botanical gardens) and observations from anatomical sections or SEM micrographs in Cistaceae, Cochlospermaceae, Bixaceae, Diptero-carpaceae, Sarcolaenaceae, Sphaerosepalaceae, and Berberidopsidaceae]. We had also at hand the extensive anatomical slide collection of the third author. Uncertain cases with regard to the presence or absence of oxalate crystals and to ovule anatomy were resolved by careful observation of selected slides (e.g., oxalate crystals seem to be absent from *Amborella*; see also Metcalfe, 1987).

We used the characters that we considered to contain the most significant phylogenetic information. Floral developmental information could only be scored with two characters (characters 223 and 224 in the matrix) due to the complexity of comparing developmental data. Characters were grouped into the following classes: 1. Serology (16 characters); 2. Chemical compounds (88 characters); 3. Characters at cellular level (22 characters); 4. Embryology (18 characters); 5. Seed anatomy (21 characters); 6. Stem morphology and anatomy (24 characters); 7. Leaf characters (17 characters); 8. Floral and fruiting characters (46 characters). The procedure of assigning character-states to taxa is documented in more detail in Appendix 5, but in general the hypothesized plesiomorphic state was used if more than one state occurred within a terminal taxon. In a few cases, paleobotanical information was also included (e.g., Magnoliaceae, Platanaceae, Buxaceae; Crane, 1989; Crane et al., 1993; Drinnan et al., 1991; Dilcher & Crane, 1984).

Most of the characters are mutually independent. Other characters were chosen as hierarchical sets (e.g., characters 8–10, 80–85, 97–100, 200–202, or 250–251), character pairs (223–224), or character triplets (108–110, 142–144). Compatibility with the molecular data set was reached by only allowing four character-states (“A,” “C,” “G,” “T”). “A” can be equated to “0,” “C” to “1,” “G” to “2,” and “T” to “3”. Characters with more than four states were broken up into character sets (233–235), but few characters required such modification.

Of the 252 characters, 207 are binary (in 186 of these simple presence/absence coding is involved) and 45 are multistate characters. The common strategy of character-state assignment described in Appendix 5 was to find a basal pattern for each taxon. With this procedure, we tried to reduce character radiation due to the evolutionary processes within the terminal taxon. In characters with states that have low probability to be evolved, due to their complexity, presence of a state was favored in coding over absence of a state (e.g., presence of phloem stratification; 169; presence of bixoid exotegmen in the chalazal region; 159; presence of salicoid leaf dentation; 201). This implied that the character was coded as being present if at least one representative of the terminal taxon is known to exhibit the character-state. By analogy, for dithetic characters, in which both states are more or less equally likely to have evolved, the character was coded as polymorphic if both character-states occur in a terminal taxon (e.g., successive or simultaneous microsporangogenesis; 128). More specific rules, which were rarely applied to cover more complex hypotheses of character evolution, are given in Appendix 5. These exceptions were applied restrictively, since the number of assumptions prior to analysis of data should be low. Appendix 5 also lists characters for which the putative ancestral character-state was searched by scoring the character-state in putatively basal members of the terminal taxon (e.g., Ulmaceae in Urticales, *Ceratonia* in Fabaceae, *Erythrospermum* in Kiggelariaceae).

Biochemical characters were scored as absent, present, or “?” (unknown or uncertain) in certain terminal taxa by considering the extent of knowledge of the biochemical substance classes in question (in the specific taxon). In wood anatomy, the broadly acknowledged evolutionary trends (see e.g., Carlquist, 1988a: chapter 11) from ancestral to derived character-states were used strictly to find character-states of terminal taxa [i.e., uni- or biseriate circular or scalariform vessel side-wall pitting was preferred over opposite, and opposite over al-

ternate (184); vessellessness was preferred over presence of vessels (integrated in 185); scalariform perforation plates were preferred over mixed scalariform and simple plates, and the latter over simple plates (185)].

All characters were scored as unordered. Ambiguous characters for which no priority rule was applied (see Appendix 5) were coded as polymorphic. Assignment of character-states was complicated by the fact that often only the presence (and not the absence) of a character-state is noted in the literature. If one or more thorough published studies of a character class in a certain terminal are available, and a given character-state was not described, it was coded as being absent. This rule was applied to, for example, presence or absence of exotegmic palisades or exotegmic longitudinal fibers in seeds (157). Some extrinsic characters such as hostplant and paleobotanical data were not included in the matrix, but their optimization was evaluated from the trees produced.

Information on taxon circumscription, characters and character-states (including four data errors that were detected after all analyses were completed), character definitions, procedures of character-state assignment, and sources are given in Appendices 2–6. The four errors were examined for effects by initiating searches on the trees found; we found no additional or shorter trees, so we assumed that complete new searches were not warranted.

In Search I, 100 random-addition replicates were run using TBR branch swapping (Swofford, 1993), but keeping only 10 trees per step (TBR = tree bisection-reconnection). The first tree of the shortest tree set obtained was swapped to completion (i.e., MULPARS turned on; Swofford, 1993). The steepest descent option (Swofford, 1993) was not used. This island that was found (sensu Maddison, 1991) contained 136 trees of length 3546, consistency index (CI) = 0.09, and retention index (RI) = 0.41.

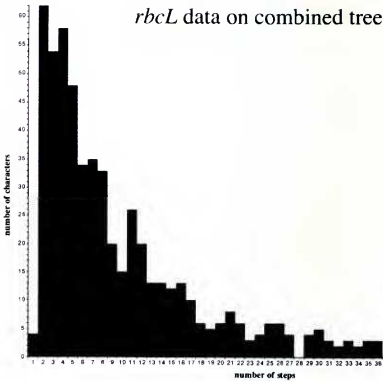
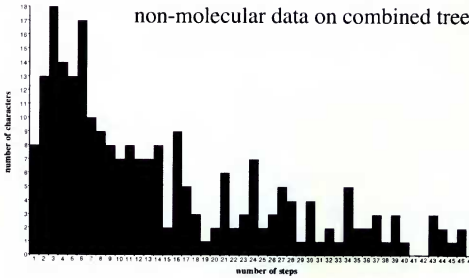
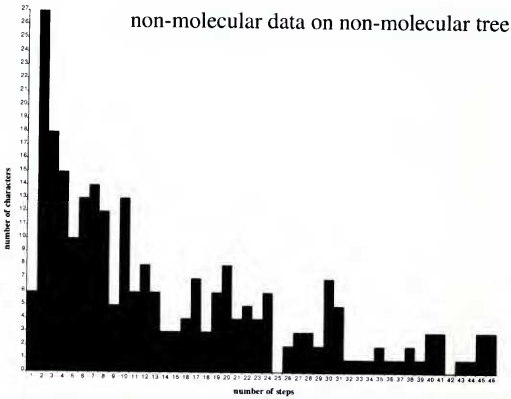
In Search II, 1000 random-addition replicates were run using SPR algorithm and keeping only 1 tree per step (SPR = subtree pruning-regrafting; Swofford, 1993). The shortest tree was swapped to completion with MULPARS turned on. The steepest descent option was not used. The resulting island

obtained with this method contained 8 trees of length 3545, CI = 0.09, and RI = 0.41.

These two searches were very slow (much slower than the *rbcL* and combined searches), and we suspected that shorter trees could be produced by another strategy, described below.

In Search III, the taxa were divided into three groups. Group I contained taxa 1 to 37 (presumed magnoliids, lower eudicots, and caryophyllids). Group II contained taxa 38 to 106 and taxa 149, 150, 161 (presumed rosids). Group III contained taxa 107 to 148 (presumed asterids). First, group II was processed. One hundred random-addition replicates were done using the TBR algorithm and keeping maximally 10 trees per step. The topology of the strict consensus of the shortest tree set (containing two most-parsimonious trees) was defined as a constraint framework for the following step. The taxa of group I were added. One hundred random-addition replicates were done with TBR swapping and keeping maximally 10 trees per step. After this, the constraints were omitted and all taxa of the first tree of the shortest tree set obtained were allowed to swap freely to completion using the TBR algorithm. The resulting tree set was defined as a constraint for the following step, with the taxa of group III added. One hundred random-addition replicates were done with TBR swapping but keeping maximally 10 trees per step. The constraints were omitted again, and all taxa of the first tree of the shortest tree set obtained were allowed to swap freely to completion using the TBR algorithm. The trees obtained were 3544 steps long. This tree set was reweighted based on the rescaled consistency index with maximal weight of 10. Twenty steps of length reduction were done with this new weight set using the TBR algorithm. After this, all characters were again weighted equally. The trees obtained in the last procedure were swapped to completion. More than 2200 trees of length 3541 were obtained. The search was stopped due to memory constraints. The first 50 trees of the obtained tree set were reweighted based on the rescaled consistency index with maximal weight of 100. Twenty steps of length reduction were done with this new weight set using the TBR algorithm. Afterward all characters were again weighted equally. The trees obtained in the

Figure 1. As evidence in support of the use of successive weighting, we used MacClade 3.06 (Maddison & Maddison, 1992) to plot how many steps were contributed by informative characters in each data matrix. In part B, for example, eight characters in the non-molecular matrix were changing one time when these data were optimized on the combined tree, whereas one character was changing 60 times. —A (top). The non-molecular data optimized on one of the shortest trees found with the non-molecular data only. —B (middle). The non-molecular data optimized on a tree from the combined analysis. —C (bottom). Plot of the *rbcL* data mapped onto the combined tree.



last procedure were swapped to completion. The steepest descent option was also not used in Search III. An ultimate tree set of 17 trees with a length of 3539, CI = 0.09, and RI = 0.41 was obtained; the first tree of this set is illustrated in Figure 2. Arrows indicate groups not found in all 17 trees. This is obviously only one island of many that exist for this data set, but it is the shortest tree length that we were able to obtain, and in spite of the unorthodoxy of the procedure, it produced far shorter trees than any "standard" method (i.e., with replicates of random taxon-addition). The three taxon-groups in Search III were formed by comparison with *rbcL* topologies. This introduces some bias in the non-molecular trees, but the application of these three groups was responsible for finding the shortest trees.

#### MATRICES FOR *rbcL* AND COMBINED DATA

The techniques involved in collecting our *rbcL* data have been previously published (Chase et al., 1993; Chase et al., 1995). Because each *rbcL* sequence represents a specific single plant (Appendix 7), which we assume can represent its family or other higher taxon, we used a single *rbcL* sequence to represent each of the terminals scored in the non-molecular matrix. In general, we selected as the *rbcL* representative a species that was not especially sequence-divergent within its group. Many of the sequences included in the present study are previously unpublished. We analyzed this new *rbcL* matrix to be certain that we could obtain results similar to those of other published *rbcL* topologies. Taxa for which we still have no molecular data are marked with "\$" in Figure 4 A, B.

Problems in amalgamating nucleotide and non-molecular data sets are discussed in Chase et al. (1995). The main problem is that non-molecular characters were scored for higher taxa whereas each *rbcL* sequence represents a single plant. In our experience, this technique does not appear to produce spurious results (several such studies have been published and more are in progress in the laboratory of M. Chase; Chase et al., 1995; Gadek et al., 1996; Morton et al., 1997). The trees obtained with more taxa, thus spanning the divergence levels present within a family, do not produce wildly different patterns, nor does substitution of one species in a family for another greatly affect the position of the family (provided the family is monophyletic). This fact is obvious when one compares the patterns found for multiple members of a family in the 1993 *rbcL* tree (Chase et al.) with the position of that family in the present analysis, in

which only one taxon was included. Furthermore, there should be no expected correspondence between a morphologically plesiomorphic taxon and plesiomorphic molecular characters, so taxon selection based on presumed "basalness" is not an important consideration. However, if faced with a choice between species that are highly divergent and others that are only slightly divergent, then use of one of the latter is helpful in avoiding spurious placements of the family.

We excluded the first 27 base positions at the 5' end of *rbcL*, leaving a maximum of 1401 basepairs (bp) of data for each species (some were less than this, although none substantially less than 1300 bp). Of these 1401 sites, 785 (56%) were variable and only 562 (40%) were potentially informative.

We used 1000 replicates of random-taxon entries and the TBR-swapping algorithm; only five trees were retained per step, which reduces the amount of time spent swapping on trees from suboptimal tree islands (Maddison, 1991). Although all trees shown were produced by successive weighting, we have shown them with their Fitch branch lengths (Fitch, 1971; i.e., characters with equal weights, character-states unordered) in Figures 3 and 4. In all but the strictly non-molecular matrix, we employed successive weighting to down weight or eliminate the effects of characters that changed excessively (Farris, 1969; Carpenter, 1988, suggested that successive weighting should be used merely to select a subset of the trees found with equal weights). To illustrate the reasons why we favor the use of successive weighting, we plotted the number of steps vs. the number of characters in MacClade 3.06 (Maddison & Maddison, 1992) for both the non-molecular and the *rbcL* matrices (both on the combined tree and on the shortest non-molecular trees). Once excessively homoplasious characters were down weighted, it was logical not to use those characters in estimating internal support. Hence relative weights were employed in the bootstrapping procedure (5000 replicates for each matrix) except for the non-molecular matrix, which was evaluated with equal weights. The rescaled consistency index (RC; Swofford, 1993) was used to calculate the successive weights (with a base weight of 1000) based on the best fit in any tree for each character, and in bootstrapping characters were sampled with equal probability rather than having the frequencies depend on the weights. We used a "fast" bootstrapping procedure in which a minimal amount of NNI swapping was used (the fastest and most superficial of the PAUP swapping algorithms; we permitted only 20 trees to be retained at each step). This procedure obviates the need to swap

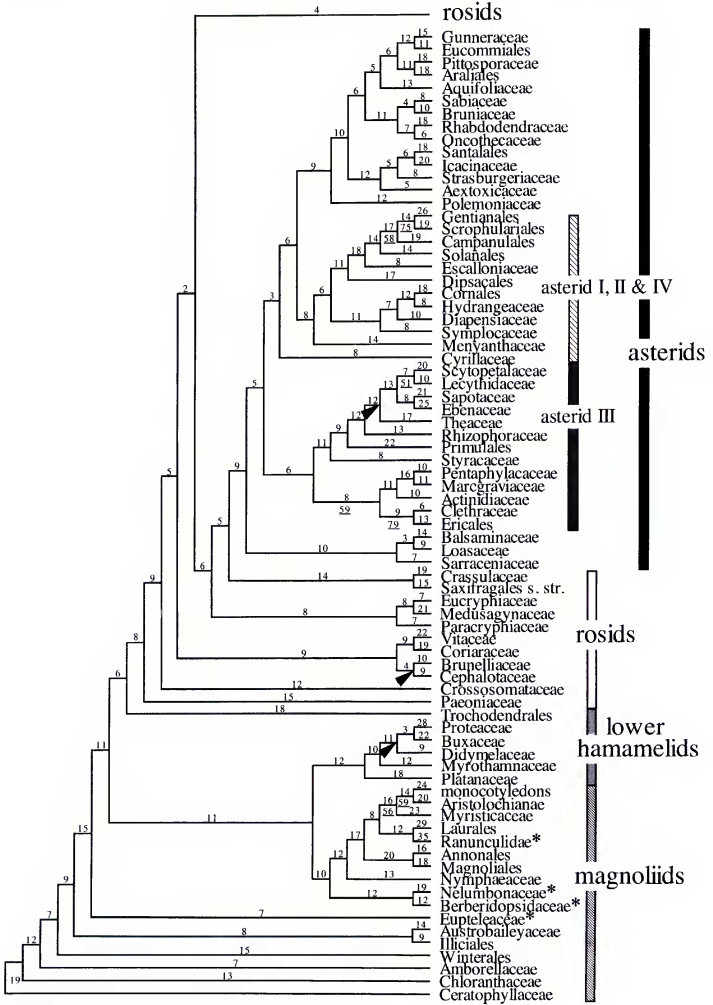
extensively, significantly shortening the time to carry out bootstrapping. Well supported groups are present in the starting trees (due to the quick distance-based calculations that PAUP and other parsimony programs use to generate a tree upon which swapping is then carried out) and do not need any swapping to be identified. If extensive swapping is required to "find" groups, then they are obviously weakly supported or unsupported; groups with intermediate levels of support necessitate at least some swapping to be effectively evaluated, hence the limited use of NNI swapping. We expect that the use of successive weighting will in many cases, as here, find trees for which the Fitch lengths (equal weighting) are longer than for the shortest trees found with Fitch parsimony. This is due to the fact that when highly homoplasious characters are down weighted, more consistent characters (those with higher relative weights) will be optimized more parsimoniously, thus forcing more changes into already highly homoplasious characters because such actions actually reduce the weighted tree length. Some characters in these matrices do change excessively often (see Results below), and thus it seems logical to us that once we have eliminated the effects of highly variable characters in the tree search procedure, these weights should be employed as well to evaluate internal support. Characters that change as often as 40–60 times should be eliminated from consideration; it seems obvious to us that these characters are not useful at this taxonomic level. In the interests of retaining a reasonable lack of a priori sifting of characters, we kept all characters until the initial patterns obtained indicated a lack of appropriateness of some data (such winnowing is of course not possible with DNA data unless one resorts to whole-category weights, and we do not find any evidence that such weighting schemes are appropriate; Chase et al., 1995, found that third codon positions in *rbcL* were better phylogenetic data than first or second positions).

## RESULTS

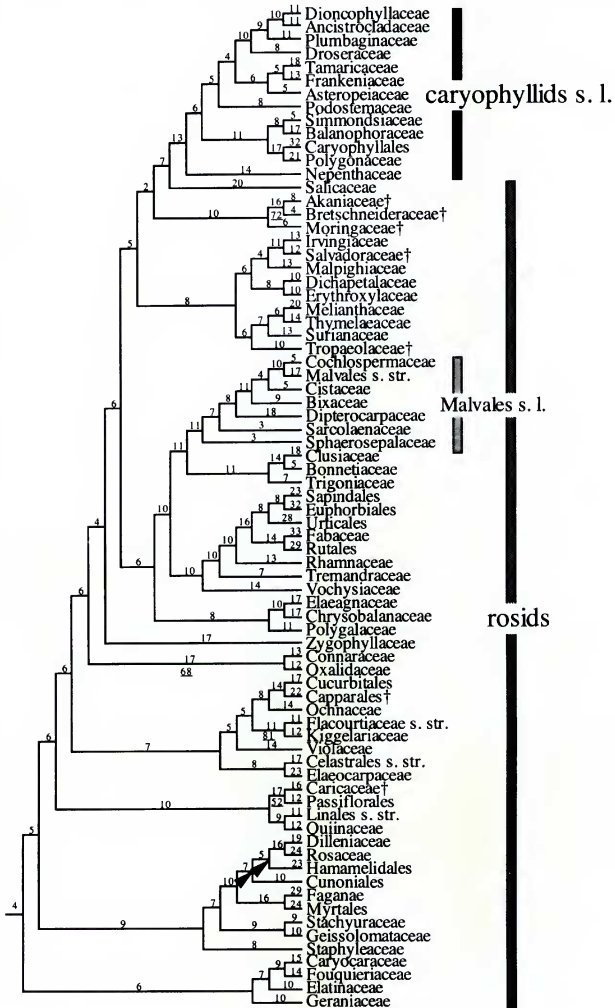
### AMOUNTS OF HOMOPLASY

The numbers of times each character of the non-molecular or of the molecular matrix changed on different trees are illustrated in Figure 1. As estimated on the combined tree found with successive weighting, some characters in the non-molecular matrix were changing up to 60 times (Fig. 1B); in the *rbcL* matrix, fewer sites were changing as frequently, although one site did change 57 times (Fig. 1C). For the non-molecular data, 26.0% of the characters changed five times or less (Fig. 1B; versus 30.3% on the shortest non-molecular tree, Fig. 1A), and 26.4% of the *rbcL* characters fell into this same category. Examples of non-molecular characters that changed frequently are distributed among different character types; pollen: polar pollen diameter (131) changed 45 times, and sexine texture (135) changed 45 times; seed anatomy: ovular or seed vascular bundles (145) changed 45 times, and embryo size (163) changed 45 times; wood anatomy: wood parenchyma (174) changed 46 times; fruits: seed to carpel number (249) changed 45 times. None of the serological or chemical characters changed more than 28 times. Both molecular and non-molecular data had nearly the same percentage of reasonably non-homoplasious characters, but many of the non-molecular characters possessed only two alternate states; therefore when these characters change two or more times homoplasy is involved, whereas base positions in DNA sequences can change up to three times without producing any homoplasy (e.g., from A to C, A to G, and A to T). Thus this comparison of percentages of numbers of steps is not entirely accurate, but the complexity involved in comparing multi-state with binary patterns is too high to be discussed here. It should be noted that with successive weighting of nucleotides based on the RC those changing three times uniquely (e.g., from A to C, A to G, and A to T) retain the same weight as those changing only once, whereas binary characters that change three times will be drastically down weight-

Figure 2. One of seventeen equally most-parsimonious trees derived from the non-molecular matrix in Search III found with equally weighted characters. These trees have 3539 steps with CI = 0.09 and RI = 0.41. Branches not found in all seventeen trees are marked with an arrow. Numbers above the branches are the numbers of estimated substitutions (ACCTRAN optimization). Underlined numbers below branches are bootstrap values; branches without an underlined number had bootstrap percentages of less than 50%. —A (left). First-branching portion of the tree, arranged with Ceratophyllaceae as the outgroup. Magnoliids and hamamelids form a grade, out of which most of the eudicots are derived. Within eudicots, rosids form a grade in which the asterids and Caryophyllids are embedded. —B (right). Mostly rosid, derived clade. \*Triparturate taxa embedded within uniaperturate grade. †Glucosinolate-producing taxa.







ed. The main point here is that successive weighting is based on the rescaled consistency index. This permits the dissection of patterns of change more accurately than merely eliminating base positions that change excessively. Weighting with the RC is also much more appropriate for DNA sequences than simple weighting with CI. Furthermore, merely eliminating all characters that change more than a certain arbitrarily set number of times (e.g., more than ten times) will eliminate some characters with multiple states (e.g., nucleotides) that retain a great deal of signal.

#### NON-MOLECULAR DATA MATRIX AND TREES

In the construction of the non-molecular matrix, some original observations, mainly in Malvales and Violales, were made. The observations on the placement of Cistaceae applying cladistic methods are convincingly supported by specialized synapomorphies. A seed with a specialized structure in the chalazal region (an exotegmic palisade layer curved inward at the chalaza, and with a hypostase plug fitting into this dome-shaped curvature), was found in the seeds of several taxa (159). We termed this chalaza structure a bixoid chalaza (Nandi, 1998a). The occurrence of this chalaza type was known for Bixaceae, Cochlospermaceae, and Cistaceae. We found it also in Pakaraimaceoideae and Monoitoidae (Dipterocarpaceae) and in Sarcolaenaceae (the character-state for Sarcolaenaceae was not included in the data matrix because it was found after the processing of the matrix). In Flacourtiaceae, salicoid leaf dentation (201, definition see Appendix 4) was found in twelve more genera not previously known to exhibit this condition: *Dissomeria*, *Byrsanthus*, *Calantica*, *Carriera*, *Flacourtia* (only some species), *Homalium*, *Ludia* (not well developed), *Oncoba*, *Poliathyrsis*, *Scopia*, *Trimeria*, and *Xylosma*.

One of the 17 most-parsimonious trees (the first one found during the search) from Search III of the non-molecular analysis is shown in Figure 2. It has a length of 3539 steps, CI = 0.09, and RI = 0.41. Branches not found in all 17 trees are indicated by solid arrows. Judging from the bootstrap results, internal support for this topology is weak; only eleven groupings received bootstrap support of 50% or greater: Myristicaceae/Aristolochianae/monocotyledons (56%), Aristolochianae/monocotyledons (59%), Clethraceae/Ericales/Actinidiaceae/Pentaphylacaceae/Marcgraviaceae (59%), Clethraceae/Ericales (79%), Scytopetalaceae/Lecythidaceae (51%), Campanulales/Gentianales/Scrophulariales (58%), Gentianales/Scrophulariales (75%), Carica-

ceae/Passiflorales (52%), Connaraceae/Oxalidaceae (68%), Flacourtiaceae s. str./Kiggelariaceae (81%), and Akaniaceae/Bretschneideraceae (72%).

Dilleniids sensu Takhtajan (1966) and Cronquist (1981) were not recovered in this analysis, and we thus treat the eudicots as being composed of ranunculids, hamamelids, caryophyllids, rosids, and asterids; we use the narrower categories (i.e., asterid I, rosid II, etc.) as necessary.

New groupings that are similar to those obtained from *rbcL* studies are a grade containing Illiciales, Austrobaileyaceae, and Amborellaceae (magnoliid II), a clade containing Magnoliales, Laurales, Annonales, Aristolochianae, and monocots (magnoliid I), a lower hamamelid group, a number of subgroups of asterids (e.g., a similar asterid III clade containing Scytopetalaceae, Lecythidaceae, Sapotaceae, Ebenaceae, Theaceae, Primulales, Styracaceae, Marcgraviaceae, Actinidiaceae, Clethraceae, and Ericales), an expanded caryophyllid group, a Malvales s.l. group, a partial Malpighiales grade containing Quiinaceae, Linales s. str., Passiflorales, Violaceae, Kiggelariaceae, Flacourtiaceae s. str., and Ochnaceae, as well as some smaller clades (Hydrangeaceae-Cornales, Lecythidaceae-Scytopetalaceae; Pittosporaceae-Araliales; Geissolomataceae-Stachyruaceae; Connaraceae-Oxalidaceae). Chloranthaceae appear consistently as an isolated family.

The uniaperturate magnoliids plus the monocots form a grade and not a clade, although a large portion of them do form a monophyletic group. The early-branching taxa include Chloranthaceae, Amborellaceae, Winterales, and Illiciales/Austrobaileyaceae; if the root belongs elsewhere, then Ceratophyllaceae would be a member of a group with these taxa. Certain triaperturate groups (i.e., eudicots) also fall into this grade; these include most of the "lower" hamamelids, plus Ranunculidae, Nelumbonaceae, Berberidopsidaceae, and Eupteleaceae (Fig. 2A). The rosids also form a grade that gives rise on the one hand to the asterids and on the other hand to the expanded caryophyllids (Caryophyllidae s.l.). The composition of Caryophyllidae s.l. is remarkable in the number of groups never associated previously as a whole in any traditional classification with Caryophyllales (Fig. 2B). These include Dioncophyllaceae, Ancistrocladaceae, Droseraceae, Nepenthaceae, Tamaricaceae, Frankeniaceae, Asteropeiaceae, Podostemaceae, Simmondsiaceae, and Balanophoraceae.

An expanded Malvales complex (Malvales s.l.) is present among the rosids (Fig. 2B), but many other groupings within the rosids found in *rbcL* trees are not evident in the non-molecular trees. In particular, the smaller groupings of rosids (rosids I, II, III)

are not evident, nor are the clades composed of glucosinolate-producing (Rodman et al., 1993) or nitrogen-fixing families (Soltis et al., 1995b).

The composition of the expanded asterid assemblage contains many of the same groupings seen in the *rbcL* trees, in particular the asterid III grouping composed of Ericales, Ebenales, Primulales, and some Theales. In addition, several other taxa are also present here that would not be expected, either on the basis of molecular studies or previous taxonomies. These include Gunneraceae, Sabiaceae, Santalales, Oncothecaceae, Aextoxicaceae, Bruniaceae, and Rhabdodendraceae.

*rbcL* TREES

The Fitch search of the *rbcL* matrix produced more than 5000 trees of 6057 steps, CI = 0.22, and RI = 0.43 (the search was discontinued at 5000 trees because the memory was becoming too low; all 5000 were swapped on to completion). Several characters changed more than 40 times (Fig. 1C). After down weighting by the use of successive weighting only nine trees were found. These nine had 6091 Fitch steps, CI = 0.22, and RI = 0.42 (weighted length of 531,123 steps, CI = 0.62, RI = 0.65). Branches not found in all nine weighted trees are marked with arrows (Fig. 3A). The first tree found at this length is illustrated in Figure 3 (ACCTRAN optimization). These trees are in general agreement with the results of Chase et al. (1993). The magnoliids form an unsupported monophyletic clade (bootstrap of less than 50%) that is sister to all eudicots, which are strongly supported (97%). Within the magnoliids, Laurales are sister to the monocotyledons; this is different from either of the two searches presented in Chase et al. (1993), but the present study uses different taxa, and in all cases this grouping is unsupported in the present *rbcL* tree (bootstrap of less than 50%). The relationship between Annonales, Magnoliales, and Myristicaceae has some bootstrap support (63%). Weak support (56%) is also shown for the association of the strongly supported pairs Nymphaeaceae/Amborellaceae (92%) and Illiciales/Austrobaileyaaceae (98%).

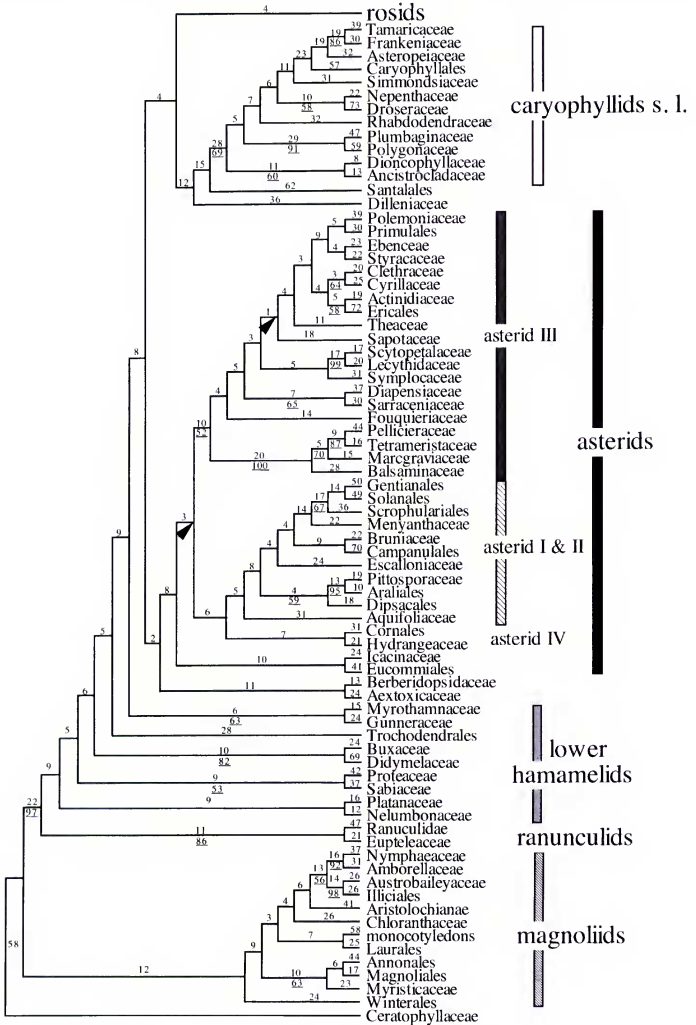
Ranunculidae/Eupteleaceae (supported at 86%) are sister to the rest of the eudicots. The lower hamamelids form a grade between Ranunculidae/Eupteleaceae and asterids/caryophyllids/rosids. Among hamamelids, Buxaceae are strongly supported (82%) as sister to Didymelaceae; Sabiaceae and Proteaceae are weakly supported (53%) as a clade. The clade of Gunneraceae/Myrothamnaceae is also supported to a similar degree (63%). Berberidopsidaceae/Aextoxicaceae form a pair without internal support, which is the sister group to the rest of the asterids.

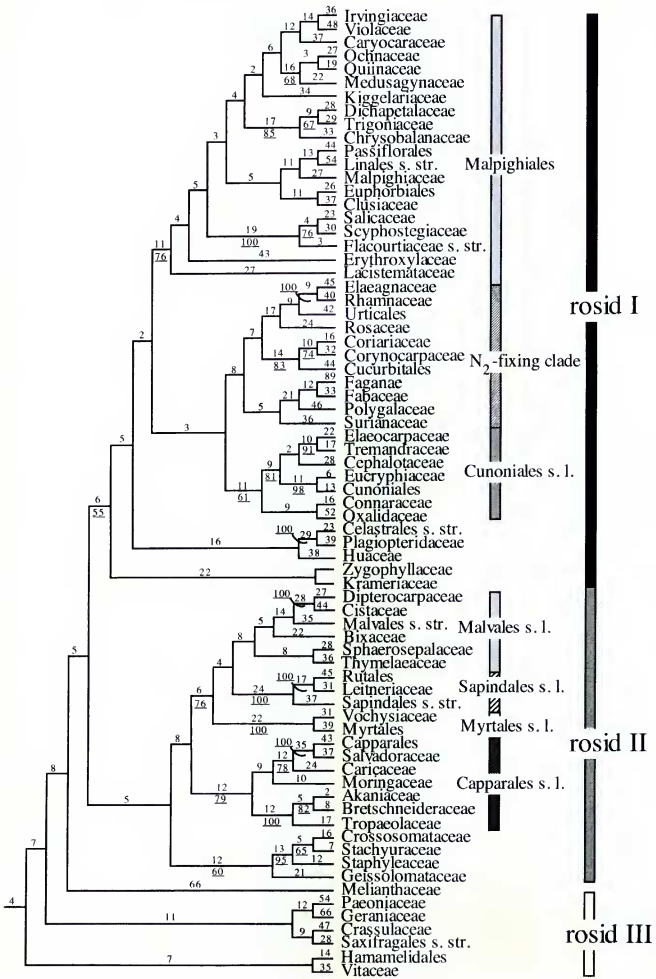
The only newly added family that falls into the asterid I and II clades is Icacinaceae. Within the asterids, Gentianales/Solanales/Scrophulariales are weakly supported (67%), as is a relationship of Dipsacales (59%) to Pittosporaceae/Araliales, a pair which has high support (95%). In general, this analysis of *rbcL* does not recover exactly the same relationships within the asterid I and II groups as in Chase et al. (1993), but the sampling is much more sparse here. The asterid IV group of Cornales/Hydrangeaceae is also recovered, but is not supported by the bootstrap.

The asterid III grouping is weakly supported (52%), and there are additional families comprising this group that were not covered in Chase et al. (1993). These include Pellicieraceae, Tetrameristaceae, and Marcgraviaceae, which are strongly supported (100%) in a clade including Balsaminaceae; the first two are also strongly supported (87%) as sister families. Lecythidaceae and Scytopetalaceae are also strongly supported (99%) as sister families, but other recent research (Morton et al., 1997) demonstrated that the latter is embedded in the former. Diapensiaceae are weakly supported (65%) as the sister of Sarraceniaceae, and the pairs Ericales/Actinidiaceae and Clethraceae/Cyrtaceae are also weakly supported (58% and 64%, respectively).

The expanded caryophyllid clade first identified in Albert et al. (1992) and further investigated in Williams et al. (1994) received weak internal support in this analysis (69%). Additional newly identified members of this clade include Tamaricaceae/

Figure 3. One of nine equally most-parsimonious *rbcL* trees found with successive weighting. Branches not found in all nine trees marked with an arrow. These trees have 6091 steps (Fitch length; i.e., equal weights) with CI = 0.22 and RI = 0.42. Numbers above the branches are the numbers of estimated substitutions (ACCTRAN optimization). Underlined numbers below branches are bootstrap values; branches without an underlined number had bootstrap percentages of less than 50%. —A (left). First-branching portion of the tree, arranged with Ceratophyllaceae as the outgroup. Magnoliids form a clade that is sister to the eudicots. Within eudicots, ranunculids and hamamelids form a grade in which the asterids are sister to the caryophyllids/rosids (for rosids, see Fig. 3B). —B (right). Rosid clade. Note that the glucosinolate and nitrogen-fixing families form clades.





Frankeniaceae (supported at 86%), Asteropeiaceae, Simmondsiaceae, Rhabdodendraceae, and Dioncophyllaceae/Ancistrocladaceae (supported at 60%). Polygonaceae/Plumbaginaceae are strongly supported (91%).

Within the rosoid clade (Fig. 3B), the same three major groups as in Chase et al. (1993) were recovered, but only rosoid I (55%) has any bootstrap support, and rosoid III is a grade (Hamamelidales pair with Vitaceae). The rosoid I group includes several newly sequenced families: Caryocaraceae, Clusiaceae, Corynocarpaceae, Dichapetalaceae, Elaeagnaceae, Flacourtiaceae s. str., Kiggelariaceae (the cyanogenic glycoside-producing genera of Flacourtiaceae s.l.), Lacistemataceae, Medusagynaceae, Plagiopteridaceae, Quiniaceae, Salicaceae, Scyphostegiaceae, and Surianaceae. Within the rosoid I clade, Plagiopteridaceae are strongly supported (100%) as the sister family of Celastrales s. str. (with more sampling, the former are embedded within the latter; Savolainen & Chase, unpublished). Elaeagnaceae/Rhamnaceae are strongly supported (100%), and Cucurbitales/Corynocarpaceae/Coriariaceae have a moderate bootstrap (83%). The Cunoniaceae clade (61%) comprises Oxalidaceae, Connaraceae, Eucryphiaceae/Cunoniaceae (98%), Cephalotaceae, and Tremandraceae/Elaeocarpaceae (91%); all but the first two listed have moderate support as a clade (81%).

Within the moderately supported Malpighiales clade (76%), Salicaceae, Scyphostegiaceae, and Flacourtiaceae s. str. are also strongly supported as a clade (100%); with increased sampling the first two families are embedded within the last; Chase et al., 1996). Chrysobalanaceae/Dichapetalaceae/Trigonaceae have moderate bootstrap support (85%), and Ochnaceae/Quiniaceae/Medusagynaceae have weak support (68%).

The composition of the rosoid II group is more or less like that in Chase et al. (1993), except that it includes Myrtales/Vochysiaceae and leaves out Geraniaceae, which appear in rosoid III instead. There is no internal support for this clade, but it is recovered in all most-parsimonious trees. Several new families (since Chase et al., 1993) are represented: Bixaceae, Cistaceae, Geissolomataceae, Salvadoraceae, Sphaerosepalaceae, Staphyleaceae, Stachyuraceae, and Thymelaeaceae.

Crossosomataceae/Stachyuraceae/Staphyleaceae/Geissolomataceae is supported at 60% bootstrap level, and within this clade, a subclade of the last three is strongly supported (95%). The mustard-oil clade has moderate support (79%), and within it Tropaeolaceae/Bretschneideraceae/Akaniaceae is strongly supported (100%; the last two at 82%) and

Caricaceae/Salvadoraceae/Capparales has moderate bootstraps (78%; the last two at 100%). Vochysiaceae/Myrtales is strongly supported at 100%, and this pair has moderate support (76%) as the sister of Sapindales/Rutales/Leitneriaceae (100%) plus Malvales s.l., comprised of Dipterocarpaceae/Cistaceae (100%), Malvales s. str., Bixaceae, Sphaerosepalaceae, and Thymelaeaceae.

As mentioned above, the rosoid III group forms a grade and contains in addition to those families identified in Chase et al. (1993), Geraniaceae and Vitaceae. With more sampling, Geraniaceae are placed near Crossosomataceae. Dilleniaceae, Melianthaceae, and Santalales are not clearly associated with any other lineage.

#### COMBINED TREES

Analysis of the combined matrix with equal weights produced only 40 trees of 10,183 steps, CI = 0.16, RI = 0.39. As with *rbcl* alone, many characters changed excessively and so we employed successive weighting, which produced a single tree (Fig. 4) with the length of 10,271 Fitch steps, CI = 0.16, and RI = 0.38 (weighted length 631,329, CI = 0.56, RI = 0.63). In general, this topology is like that for *rbcl*, but there are a number of differences. The differences of the combined tree from the non-molecular trees are more substantial, as are the differences between the *rbcl* and the non-molecular trees. The major differences of the combined from the *rbcl* trees are as follows: the magnoliids form a grade rather than a clade; the ranunculids are sister to one of the clades, Platanaceae/Nelumbonaceae, that make up the hamamelid grade; the Caryophyllids are sister to a combined rosoid/asterid clade, in which these are monophyletic sister groups; Malvales s. str. are the sister to Bixaceae, Cistaceae, and Dipterocarpaceae in the combined tree, whereas they are placed between Bixaceae and Cistaceae/Dipterocarpaceae in the *rbcl* trees; the Bixales group with the taxa having a bixoid chalaza in their seeds (Nandi, 1998a; 159) thus appears as monophyletic in our combined tree (Sarcolaenaceae, for which no *rbcl* sequence was available, do have a bixoid chalaza; this character was found too late to be included in the matrix; if this character-state could be coded, Sarcolaenaceae would probably appear in the Bixales group as well); Fabaceae are placed outside the nitrogen-fixing clade in the combined tree; Clusiaceae are placed in a clade with Caryocaraceae, Elatinaceae (only non-molecular data), and Bonnetiaceae (only non-molecular data) in the combined tree, whereas they appear as the sister group of Euphorbiales in

the *rbcL* trees; Violaceae are found in a group that is sister to a large clade containing, e.g., Flacourtiaceae s. str. and Euphorbiales, whereas they are placed differently in the *rbcL* trees; Kiggelariaceae are sister to Flacourtiaceae s. str., Scyphostegiaceae, and Salicaceae in the combined tree, whereas they are more distant from Flacourtiaceae s. str. in the *rbcL* trees.

The addition of the non-molecular data to the *rbcL* matrix greatly reduced the number of trees obtained; in the case of the Fitch analysis it dropped from more than 5000 (at which point the memory was exhausted) to only 40, and in the weighted analysis from nine to only one. If there were agreement between patterns in the molecular and non-molecular data, then an effect of increased support might be observed in the combined analysis. This is partly the case, but the amount of missing data in the non-molecular analysis makes this assessment difficult; there are many exceptions noticed by comparing Figures 3 and 4. For example, support for an expanded Nymphaeales (including Amborellaceae, Austrobaileyaceae, and Illiciales) decreases slightly (from 56% to 53%), but the support for the two pairs, Nymphaeaceae/Amborellaceae and Illiciales/Austrobaileyaceae, decreases markedly, from 92% and 98% to 86% and 75%, respectively. Citing all such cases is not a worthwhile endeavor at this stage of investigation. At the least, it can be stated that the addition of the non-molecular data does not drastically alter the pattern obtained with *rbcL* alone, nor does it greatly decrease bootstrap support.

TAXA IN THE *rbcL* TREES FOR WHICH INSUFFICIENT  
NON-MOLECULAR DATA ARE AVAILABLE

A number of small families have been included in the non-molecular matrix, but little information is available for them. The presence of such taxa can destabilize results and produce lower levels of internal support. Most of these taxa received strong support for placement in the *rbcL* trees, and they seem relatively securely placed in the combined tree. We point out these taxa here to draw attention

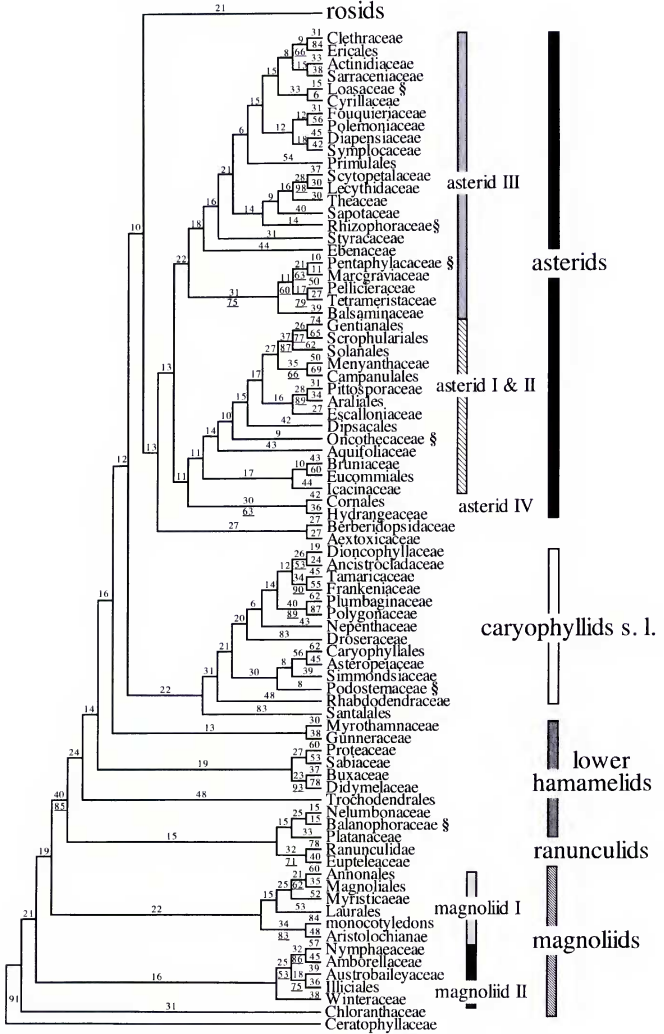
to them: Tetrameristaceae and Pellicieraceae are found near Marcgraviaceae in the *rbcL* and combined trees (Figs. 3A, 4A) and are also sister groups tending to be placed in asterids in the non-molecular trees (Fig. 2A); Corynocarpaceae falls in the clade formed by Coriariaceae and Cucurbitales (including Datisceae and Begoniaceae) in the *rbcL* and combined trees; Leitneriaceae have a stable position near Rutales/Sapindales; Huaceae are placed near Celastrales s. str.; and Lacistemataceae and Scyphostegiaceae are found near Flacourtiaceae s. str.

DISCUSSION

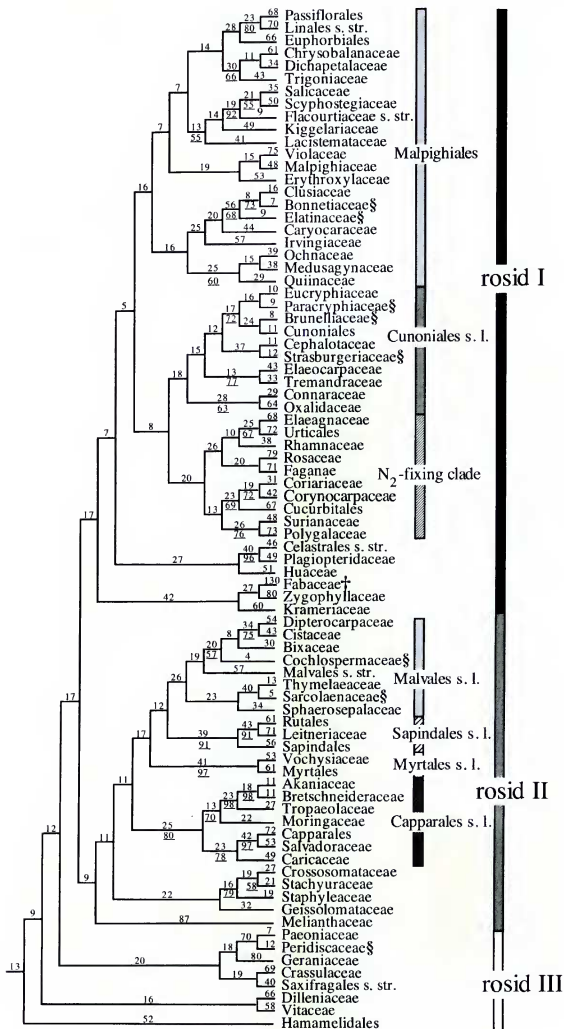
Certain caveats must be proffered before further consideration of the results of these analyses. To overcome the disadvantages of high taxon number and large amounts of missing data (which always slows the process of finding shorter trees; pers. obs.), we regrouped the taxa into three subgroups (Search III). These corresponded to what we presumed were magnoliids, lower eudicots, and Caryophyllids (group I), rosids (group II), and asterids (group III). This led to the advantage of shorter and more thorough computation and ultimately yielded trees up to six steps shorter than those found with the other two search strategies. This method is somewhat biased in presuming three major groups, but the final unconstrained swapping and reweighting procedures should compensate for the biases thus introduced. With an RI of 0.41, this matrix is highly likely to be subject to islands (Maddison, 1991), and this appeared to cause problems for standard types of search strategies. This is likely true also for the *rbcL* and combined matrices, although these were clearly more consistent in finding reasonably similar tree lengths in each of the random replicates of coding order.

The methods used for entering of the non-molecular data can be improved. Assessments of character polarity before analysis are assumption-laden. Coding only a single character that is assumed to be the plesiomorphic state for cases in which polymorphisms occur could result in spurious place-

Figure 4. The single most-parsimonious combined tree found with successive weighting. The tree has 10,271 steps (Fitch length; i.e., equal weights) with CI = 0.16 and RI = 0.38. Numbers above the branches are the numbers of estimated changes (ACCTRAN optimization). Underlined numbers below branches are bootstrap values; branches without an underlined number had bootstrap percentages of less than 50%. —A (left). First-branching portion of the tree, arranged with Ceratophyllaceae as the outgroup. Magnoliids form a grade composed of two major subclades (magnoliid I and II) with the former sister to the eudicots. Within eudicots, ranunculids and hamamelids form a grade. The Caryophyllids are sister to the asterids/rosids (for rosids, see Fig. 4B). —B (right). Rosid clade. Note that the glucosinolate and nitrogen-fixing families form clades. \*Taxa for which *rbcL* sequences were unavailable. †Nitrogen-fixing family outside the main nitrogen-fixing clade (Fabaceae).







ments of some taxa. An example of an assumed apomorphy can be seen in the results for Liliaceae in Chase et al. (1995), in which the combined *rbcL* and morphology trees indicated that an inferior ovary was the plesiomorphic condition. This is the opposite conclusion one would reach based upon generalized character trends in angiosperms, and such conclusions could result in spurious assessments of relationships. Moreover, coding terminals as polymorphic can also produce erroneous topologies (Nixon & Davis, 1991). Adding terminals would be a solution, but it would involve unmanageable matrix dimensions and the need for more specific data on variation within larger clades. For example, if a taxon B is deeply nested within a large taxon A, it would be difficult to detect this relationship with our data. Taxon B would most likely attach to a subgroup of taxon A (which in our matrix may be absent). This would mean that large taxa have to be split up. An example of this problem is our use of Rutales, Sapindales, and Leitneriaceae. With more sampling within the two orders (Gadek et al., 1996), Leitneriaceae is embedded within Simaroubaceae of Sapindales. In our trees, it appears as sister to Sapindales. Despite these caveats, the approach used here is made stronger by the inclusion of many more characters than taxa. As long as most characters are accurately scored, the general results should contain useful and new information, and the "phylogenetic signal" should not be overly distorted.

The non-molecular matrix often deals with large taxonomic units composed of many families. The results are thus meaningful only if these taxa are monophyletic. We used higher-order taxa when the results of Chase et al. (1993) and many published studies (Appendix 6) coincided with the traditional circumscription of these groups. In the *rbcL* and combined analyses, these groups were represented by only a single sequence of a representative species. The effects of using exemplars is discussed in Systsma and Baum (1996), but the results do not differ significantly from other *rbcL* studies using more than single representatives.

A different approach would have been to use species as terminals, preferably the same species as covered by the *rbcL* database. This approach, however, would have the disadvantage that not all character fields would be investigated for the species or even the genus in question. Moreover, it seems most likely that the coverage of all angiosperms with exemplar species would require a sample of more terminal taxa than in this study. This again would necessitate more phylogenetically informative characters. This species-terminal ap-

proach, at the present time, is impractical and could not be effected; there simply are not enough species studied for all these characters.

We intend this study to be an example of the direction that we think phylogenetic studies should be taking. We will be most gratified if other researchers take our matrices and improve upon them. The literature is voluminous. We have surely missed a number of papers, but these matrices are now there to be completed. The gaps will be obvious to those who are interested. The missing cells need to be filled in, and we can see that if they are, there is hope for improvement. For those taxa on which we have focused most and incorporated more of the relevant literature (e.g., Malvales s.l.), the non-molecular (Fig. 2B), the molecular (Fig. 3B), and combined trees (Fig. 4B) are all highly congruent. The non-molecular results for Cochlospermaceae, Bixaceae, Cistaceae, Dipterocarpaceae, and Sarcolanaceae also demonstrate that the search for characters has to consider a wide array of subject areas.

The final caveat concerns the use of successive weighting to "improve" the matrices (Farris, 1969). Some readers will wonder how this procedure has "distorted" the results produced by equal weighting, the results of which we have not shown. All data sets contain characters that are excessively "noisy," and these can be detected by an examination of their consistency on any of the trees (Fig. 1). This is evidence that, although these characters may be useful at some hierarchical level, they are not useful at the broad scale being studied here. A priori one cannot and should not make this sort of decision; it is simply too assumption-laden. When the initial results from an analysis indicate that certain characters are relatively more inconsistent than others, then the effects of the former should be lessened and those of the latter enhanced (i.e., made more consistent). The effect of successive weighting is never vastly different from that of equal weighting; in the great majority of cases, successive weighting merely identifies a subset of the trees found with equal weights as optimal (i.e., those that favor the more consistent characters). This is not the case with any of the trees found here, but both the *rbcL* and combined results have nearly the same Fitch length as the most-parsimonious Fitch tree (the weighted trees are only 0.56% and 0.86% longer than the Fitch trees for *rbcL* alone and the combined matrices, respectively; the CI and RI for the Fitch and weighted trees are nearly identical and only differ at the third decimal point levels, CI = 0.217 versus 0.215 and RI = 0.428 versus 0.424 for *rbcL*, and CI = 0.160 versus 0.159 and RI =

0.390 versus 0.384 for the combined analysis). We attempted to use successive weighting on the non-molecular data, but, like the search protocol itself, this procedure would have occupied many months of computer time and was therefore abandoned.

#### (A) TREES AND GENERAL PATTERNS

No previous cladistic analysis of the angiosperms has used as many higher-level taxa as this, including Chase et al. (1993) and Soltis et al. (1997b), which both used more species but fewer families. Of course, many of the families are subsumed in these trees by higher-order taxa (i.e., monocotyledons, Faganae, Urticales). This process of selecting terminals did not have a great effect on topology for the *rbcL*-only analysis, which deviates only slightly from that seen in Chase et al. (1993), and our results also do not differ drastically from those produced by 18S rDNA either (Soltis et al., 1997b). Several more divergent families are differently placed, which could be due to the overall sparser sampling permitting branch attractions to occur. These families (relative to Chase et al., 1993) are: Geraniaceae, in rosid II near *Crossosoma* before, here in rosid III (Fig. 3B); Vitaceae, in an isolated position with Dilleniaceae before, here with Hamamelidales; Krameriaceae/Zygophyllaceae, near Rosaceae in rosid I before, here in an isolated position as sister to the rosid I clade; and Fabaceae, which in the *rbcL* trees falls into the nitrogen-fixing clade (Fig. 3B) but in the combined tree is sister to Zygophyllaceae/Krameriaceae.

Several taxa occupy isolated positions in the *rbcL* and combined trees, and these would appear to be critical for understanding the patterns observed in the largest clades (i.e., rosids, asterids, and Caryophyllids). These include Aextoxicaceae, Berberidopsidaceae, Dilleniaceae, Gunneraceae, Myrothamnaceae, Vitaceae, and Santalales. These taxa have shifted positions in every published large *rbcL* analysis, but they always come out as the sister taxa of the largest clades of eudicots. Within the asterids, Aquifoliaceae, Eucommiales, and Icacinaceae perform similarly; among rosids the Celastrales s. str./Plagiopteridaceae, Huaceae, Krameriaceae/Zygophyllaceae, Melianthaceae, and Crossosomataceae/Stachyuraceae/Staphyleaceae/Geissolomataceae clades are likewise unstable. Their positions in the non-molecular trees are generally different from their positions in the *rbcL* and combined trees. Aextoxicaceae, Berberidopsidaceae, Dilleniaceae, Gunneraceae, Myrothamnaceae, Vitaceae, and Santalales, those taxa that fall as sister groups of the asterids, Caryophyllids, and rosids in Figures 3 and

4, are embedded among the magnoliids or included in the rosid groups that fall apart from the main rosid clade in the non-molecular trees (Fig. 2A). These taxa have a large number of plesiomorphic traits. For example, *Berberidopsis* (Berberidopsidaceae) has an undifferentiated perianth, plesiomorphic wood (presence of mostly solitary vessels with scalariform perforation plates and opposite side-wall pitting, absence of septate fibers), and tricolpate pollen (Miller, 1975; Lemke, 1988).

The *rbcL* data contain significantly greater phylogenetic information than the non-molecular data in this broad study (e.g., they delimit more groups with greater levels of internal support). In part, this must be ascribed to the structure of the non-molecular matrix, containing many empty cells and also a larger number of polymorphisms. Moreover, it has become obvious that all larger clades of angiosperms can only be characterized by few non-molecular traits (see part b of Discussion). This results in a matrix that seems to yield only slightly longer trees using standard methods (i.e., no compartmentalization). In phylogenetics, it has been underestimated that the more "signal" (i.e., the less randomness) is contained in a data matrix, the easier it is to find optimal trees. The 1993 *rbcL* tree was obtained in a relatively short search (Chase et al., 1993); trees only five steps shorter were found by Rice et al. (1995) after many more months of search on more than one computer. The only differences between these minimally shorter trees and the trees found in 1993 concern groupings that are weakly supported regardless of their positions. Nothing more of significance has been obtained except a huge outlay of computing time and personal effort; the 1993 tree contained all of the strongly supported groupings, and represents well the phylogenetic signal present in *rbcL* data. It should be accepted that with large searches for which exact solutions are impossible (such as this and the other large angiosperm matrices) excessive swapping over several months is not reasonable; effort is better spent in finding additional data. When all groups are strongly supported, then finding the optimal solution will be easy and the trees accurate (Soltis et al., in press). Even after many additional months of search on the 1993 *rbcL* matrix, we cannot say that anything new was learned. The most that was achieved was the observation that many groups, especially those with long branches, were unstable. Of course, we performed bootstrap analyses here, and this makes the general weakness of the *rbcL* tree evident. Unpublished analyses of *atpB* for nearly 300 seed plants take even less time than *rbcL* and contain even more groups with strong sup-

port. Soltis et al. (1997b) presented 18S rDNA data for 232 seed plants. The authors reported that more time is required for 18S than for *rbcL* alone or *rbcL*-18S combined searches, and again the major problem with large data sets is not just their size, but also the degree of randomness and missing cells that they contain. The large number of question marks and lack of support in the non-molecular matrix are serious obstacles to rapid search. Likewise, they do not permit the use of the jackknife (J. Farris, pers. comm.), which is a fast and accurate method of finding groups with strong internal support, regardless of the size of the matrix (Farris et al., 1997).

Some authors have suggested that hybridization or other forms of horizontal gene transfer could have a major effect on higher level studies within the angiosperms and could be expected to create conflicts between data categories (Syvanen et al., 1989; Syvanen, 1994). Others did not give hybridization a major role at higher levels (Chase et al., 1993). We do not deny that high levels of parallelisms exist among angiosperms, but we find the explanation of widespread horizontal gene transfer as the cause (Syvanen, 1994) unappealing and not conducive to further investigation. Studies of nuclear 18S rDNA (Soltis et al., 1997b) and plastid *atpB* (Savolainen et al., 1996) find results highly congruent with those of *rbcL*. In particular, the congruent topologies found with plastid genome sequences (*rbcL* and *atpB*) as well as with nuclear genome sequences (18s rDNA) argue against hybridization being a major problem in higher level plant systematics. Reticulate evolution, dating to a time when hybridization was still possible between now distant lines, appears to have only minor effects on macrosystematic patterns (for discussion of effects leading to parallelisms, see also Kubitzki et al., 1991).

(B) NON-MOLECULAR CHARACTERS OF TAXON GROUPS  
DISCUSSED ON THE BASIS OF THE COMBINED DATA TREE  
(FIG. 4 A, B)

We argue that the trees with the greatest underlying data are the most appropriate to discuss; thus, unless specifically stated, we will discuss only the combined tree from Figure 4. We focus on a series of characters that appear to contribute to the topology obtained in the combined tree. This is not meant to be an exhaustive examination of these topics. We intend instead to illustrate some of the trends in the non-molecular data that agree with the distribution of variation in the *rbcL* matrix. Characters described are synapomorphies as yield-

ed by MacClade 3.04 on the combined tree, unless stated otherwise. Other characters that are widely represented within a clade may represent synapomorphies if the topologies are only slightly rearranged; since many of these branches are weakly supported, discussing these characters as either synapomorphies or plesiomorphies seems premature and potentially misleading. Therefore we discuss many characters as simply being widespread or frequent within clades; many of these will eventually be demonstrated to be synapomorphies. Due to the large number of missing cells and low levels of internal support with present data, it seems most prudent to consider only their relative frequencies or tendencies of occurrence rather than to frame this discussion as an investigation of synapomorphies.

*Magnoliidae.* The strict dichotomy of the leaf parts in *Ceratophyllum* is unusual in angiosperms, even if compared with other water plants showing the *Hippuris* syndrome of leaf architecture (cf. also Cook, 1978; Rutishauser & Sattler, 1987). The inflorescence is a spike with the flowers frequently arranged in two orthostichies (Raynal-Roques, 1981). This inflorescence type shows some similarities to the decussate spikes in *Chloranthus* and could reflect an old pattern. Also the flowers in *Ceratophyllum* are unisexual (Endress, 1994b), and this could be plesiomorphic for angiosperms or apomorphic as a result of adaptation to an aquatic autecology.

Chloranthaceae occupy an isolated and perhaps early-diverging position (see also Nixon et al., 1994). This is concordant with the fact that the oldest fossils known at present that are clearly attributable to angiosperms are Chloranthaceae-like. Chloranthoid pollen was described from the Valanginian of Israel (Brenner, 1996). *Hedyosmum*-like flowers are known from the Valanginian or Hauterivian of Portugal (Friis et al., 1994; Crane et al., 1995; E. M. Friis, pers. comm.) and are thus even older than the *Ceratophyllum*-like horned fruits found from an Aptian locality (Dilcher, 1989). The fact that distinct Aptian fossil material has been found that appears to combine characters of Chloranthaceae, Piperales, and Circaeasteraceae (Ranunculidae; Crane et al., 1995) indicates that early angiosperms exhibited a suite of traits that are now only known to occur individually within distinct terminal clades of extant angiosperms. The decussate arrangement of the flowers in spicate inflorescences in *Chloranthus* and the Late Cretaceous *Chloranthistemon* (Endress, 1987; Eklund et al., 1997) is paralleled by the decussate inflorescences

of *Ephedra* (Hufford, 1996). The comparison of branched male structures in Gnetales and Chloranthaceae is problematical because of unclear homologies (Endress, 1987; Friis & Endress, 1990; Doyle, 1994, 1996). For comparison of Chloranthaceae with Gnetales see also Taylor and Hickey (1996) and critical discussion by Doyle (1996) and Endress and Igersheim (1997). Also the highest diversity of pollen aperture types within an angiosperm family seems to occur in Chloranthaceae (not expressed in the characters used for this analysis; see, e.g., Erdtman, 1952). Sesquiterpenes, as  $\gamma$ -elemene, can serve to indicate relationships of Chloranthaceae to other angiosperm families. At present,  $\gamma$ -elemene is known only from Chloranthaceae, Piperaceae, and Aristolochiaceae (Hegnauer, 1962–1994). The germacrene acoragermacrene occurs only in Chloranthaceae and monocots (Hegnauer, 1962–1994). These two compounds seem to indicate an evolutionary relationship of Chloranthaceae to Aristolochianae–monocots or are a relict of previously more widespread traits.

*Amborella* also occurs in an isolated position in our non-molecular trees (Fig. 2A). *Amborella* was found as the sister group to the rest of angiosperms in a subset of the 18S rDNA trees (Soltis et al., 1997b), but in a clade supported by the jackknife along with Illiciales, Austrobaileyaceae, and Nymphaeales in the combined analysis of *rbcL* and 18S in Soltis et al. (1997a). Probably ancestral or erratic characters of *Amborella* include the presence of S-type plastids in the sieve-tubes (107), uniperturate in addition to inaperturate pollen grains (129; Sampson, 1993), minute embryos (163), scanty wood parenchyma (174), no fibers (not coded), tracheids (177), wood rays of Kribs heterogeneous type I (179), circular tracheid side-wall pitting (similar to some Gnetales; 184), no vessels (not coded; probably plesiomorphic), no discontinuous calyx-corolla transgression (210), practically orthotropous ovules (246), and stipitate fruits (239) (Metcalfe & Chalk, 1950; Behnke, 1981; Cronquist, 1981; Takahashi, 1985; Carlquist, 1988a; Endress, 1994c). Brenner (1990, 1996) reported that angiospermous, inaperturate pollen grains, which may have evolved into a *Clavatipollenites* pollen-type, are present in the Valanginian and Hauterivian of Israel. Judging from these paleobotanical finds, one may take into consideration whether the inaperturate pollen grains found in *Ceratophyllum*, *Ascarina* (Todzia, 1993), *Amborella*, *Trimenia papuana* (see Sampson & Endress, 1984), and many Laurales (Gomortegaceae, Hernandiaceae, Lauraceae, Monimiaceae except Atherospermatoidae) are reductions or represent an old, con-

served, character-state. Neglect of the presence of inaperturate pollen in the above-mentioned magnoliid taxa based on the assumption that the inaperturate condition does not represent the basal pollen type could result in different topologies at the base of the tree.

All taxa of magnoliids and early-branching eudicots included in this analysis have ovary-to-carpel length ratios greater than 1:2 (i.e., with short or absent styles; 236). The formation of long styles in relation to the whole carpel thus seems to be an apomorphic tendency in basal angiosperms. A mesotesta (middle layer of outer integument in the seed; 154) with sclerified cells is present in many magnoliids: Chloranthaceae (*Chloranthus* spp.), Nymphaeaceae, Austrobaileyaceae, Illiciales, Aristolochianae (*Aristolochia* spp.), Myristicaceae (*Horsfieldia*, *Myristica*), Annonales, Magnoliales (Corner, 1976; Endress, 1980; Takhtajan, 1988). A mechanical layer in the mesotesta is also found in some early-branching eudicots (Eupteleaceae; Buxaceae; *Sarcococca*; and Hamamelidaceae; Corner, 1976).

The clade formed by Laurales, Aristolochianae, monocots, Myristicaceae, Annonales, and Magnoliales (magnoliid I clade; Fig. 4A) shows a frequent occurrence of the phenylpropane asarone (41). Asarone is known from Lauraceae (*Sassafras*), Piperaceae (Piper), Aristolochiaceae (*Asarum*), Annonaceae, and Magnoliaceae (*Magnolia*) (Gildemeister & Hoffmann, 1956; Hegnauer, 1962–1994; Sethi et al., 1976; Keller, 1982). Outside of this clade Hegnauer (1962–1994) cited only three families of angiosperms that produce asarone. The same clade contains the only plant taxa that Hegnauer (1962–1994) and Harborne and Baxter (1993) found to produce the lignans galbacin (57) and veraguensin (59). The neolignan licarin (58), though described from *Krameria* (Dominguez et al., 1992), is also predominantly found in this magnoliid I clade (Gottlieb et al., 1988, stated that neolignans have their center of diversification in the magnolialean families). Galbacin, a tetrahydrofuranoid lignanoid, occurs in Lauraceae (*Persea*), Aristolochiaceae (*Aristolochia*), Myristicaceae (*Knema*, *Viola*), and Himantandraceae (*Galbulimima*) (Hegnauer, 1962–1994; Harborne & Baxter, 1993). Veraguensin, also a tetrahydrofuranoid lignanoid, is known to occur in Trimeniaceae (*Trimenia*), Lauraceae (*Ocotea*), Saururaceae (*Saururus*), Myristicaceae (*Viola*), and Magnoliaceae (*Magnolia*) (Harborne & Baxter, 1993). Licarin has been found in Lauraceae (*Licaria*), Aristolochiaceae (*Aristolochia*), Myristicaceae (*Myristica*), and Magnoliaceae (Hegnauer,

1962–1994; Ionescu et al., 1977; Le Quesne et al., 1980; Harborne & Baxter, 1993).

The alkaloid liriodenine (83) is known only in the magnoliid I clade, as well as in Ranunculidae and Nelumbonaceae; the last-mentioned taxa fall into the sister group of the remaining eudicots. As with two of the three lignanoids mentioned above, liriodenine is not known from any families outside of these clades, most significantly not from the magnoliid subclade containing Winterales, Nymphaeaceae, Amborellaceae, Austrobaileyaceae, and Illiciales (Hegnauer, 1962–1994; Harborne & Baxter, 1993), hereafter the magnoliid II clade (Fig. 4A). The magnoliid I clade further has sieve-tube plastids of the P-type (107) in a majority of families (Behnke, 1981), whereas all members of the magnoliid II clade except Canellaceae (here in Winterales) have S-type plastids. Aristolochianae and monocots are further linked by the common presence of crystal sand (in Piperaceae, Metcalfe & Chalk, 1989, and Araceae, but not in *Acorus*, Solereder & Meyer, 1928; Franceschi & Horner, 1980; Seubert, 1993; 115), of a dispersed vascular system (in Piperaceae and monocots, but not in Saururaceae; 167), and of frequent trimery in perianth (212–214), androecium (221), and gynoecium (233–235). Aristolochianae and monocots also cluster on the basis of the widespread occurrence of two stamen whorls (not coded). More similarities, perhaps as the result of common ancestry, are enumerated by Burger (1977) and Dahlgren and Clifford (1982). All magnoliid I families except monocotyledons/Aristolochianae share a stratified phloem (169) and wedge-shaped phloem rays (Metcalfe & Chalk, 1950; Cronquist, 1981; Carlquist, 1988a; 170).

Both the non-molecular and the combined trees show Chloranthaceae as an isolated family apart from the main magnoliid clades. Also equally isolated in all trees are Amborellaceae, Austrobaileyaceae, and Illiciales (magnoliid II clade), separated from the more typical magnoliid I clade, in which the monocots are sister to Piperales/Lactoridaceae/Aristolochianae (Fig. 4A).

**Eudicots.** Eudicots are held together by their triaperturate pollen grains (129), which most likely evolved in parallel in Illiciales (Erdtman, 1952; Doyle et al., 1990; Qiu et al., 1993).

Many early-branching eudicots have representatives with tricolpate pollen grains; these are cited here, as in Chase et al. (1993), as the ranunculids and lower hamamelids (the latter a grade composed of several small clades). These taxa are nearly all relatively small and could be considered remnants

of previously more widespread and numerous archaic lineages. In our scheme, these lineages would include Berberidopsidaceae, Nelumbonaceae, Platanaceae, Ranunculidae, Proteaceae, Gunneraceae, Myrothamnaceae, and Trochodendrales. Vitaceae and Aextoxicaceae appear to be related also to these, but exhibit some more advanced characters, such as tricolpate pollen, which is more predominant in derived eudicot lineages (see, e.g., Erdtman, 1952). In *Nelumbo*, both tricolpate and monosulcate pollen are reported (Kuprianova, 1979; Blackmore et al., 1995; coded only as tricolpate in the matrix because we became aware of the occurrence of monosulcate pollen in *Nelumbo* only after analysis). The sister group of the rest of eudicots consists of Nelumbonaceae, Platanaceae, Eupteleaceae, and Ranunculidae. A number of these families have some members with palmately veined leaves or leaves with no dominant single primary vein (i.e., Menispermaceae, Lardizabalaceae, Circaeasteraceae, Ranunculaceae, Berberidaceae, Nelumbonaceae, and Platanaceae; 198). The leaves of *Kingdonia* and *Circaeaster* are particularly interesting for their dichotomously branching venation, which is rare in angiosperms (for the conditions in *Kingdonia*, see Foster & Arnott, 1960; morphogenetic interpretations by Hagemann, 1970, and Hagemann & Gleissberg, 1996). Foster and Arnott (1960) hypothesized that the dichotomous venation pattern in *Kingdonia* represents an ancestral character-state. Imprint leaf fossils from the Early Cretaceous of Madagascar have been found that show characters similar to extant *Circaeaster* (O. Appert, pers. comm.). Circaeasteraceae and Kingdoniaceae were placed in the ranunculalean clade by Oxelman and Lidén (1995; here including *Trochodendron*) based on an analysis of 28S rRNA. They were also given family rank (as members of a distinct order in the Ranunculidae) by Takhtajan (1997).

Proteaceae and Sabiaceae are linked by the common presence of wedge-shaped phloem rays (Metcalfe & Chalk, 1950; 170) and of a nectary disk (Haber, 1959, 1961, 1966; van Beusekom, 1971; 231), a rare character in the early-branching angiosperms. Buxaceae and Didymelaceae share a simple, bract-like perianth (possibly plesiomorphic; 209) and encyclocytic stomata (195), the latter a rare character-state present in only eleven taxa of our analysis (see also Metcalfe & Chalk, 1950, 1988, 1989). Aextoxicaceae and Berberidopsidaceae are also linked by this same character (Cronquist, 1981; Baas, 1984).

Ellagic acid is not only absent from the magnoliids, with the exception of Nymphaeales (Amborellaceae have not been sampled), but also from the

first-branching eudicots, Ranunculidae, Eupteleaceae, Platanaceae, Nelumbonaceae, Proteaceae, Sabiaceae, Buxaceae, and Trochodendrales. Gallic acid (70) shows a similar distribution (Hegnauer, 1962–1994; Gibbs, 1974).

The morphological data set does not establish the sister-group position of Ranunculidae to the remaining eudicots but places them nested in the magnoliid I clade (Fig. 2A). Perhaps a better knowledge of the biochemistry of some basal eudicots (Eupteleaceae, Platanaceae, Sabiaceae, Didymelaceae) would cause a somewhat modified placement of Ranunculidae. The non-molecular trees also do not consistently separate *Nelumbo* from magnoliid I (Fig. 2A). In all trees *Trochodendron*, *Tetracentron*, Proteaceae, Sabiaceae, Buxaceae, and Didymelaceae are in an isolated position (cf. also Drinnan et al., 1994). *Berberidopsis*, a ditypic Australian–Chilean disjunct genus, shows no close relationships to Flacourtiaceae in either data set. A distinct position of *Berberidopsis* within the core-Flacourtiaceae s.l. was already indicated by Keating (1975) on the basis of pollen morphology and by Miller (1975) on the basis of wood anatomy. The *rbcL* and combined analyses place *Berberidopsis* and *Aextoxicaceae* (also from Chile) as sister to the asterids (Figs. 3A, 4A), and the non-molecular analysis places them with the magnoliid I clade (Fig. 2A).

Dilleniaceae and Vitaceae have never been considered closely related, but they share oxalate raphides (Metcalfe & Chalk, 1950; 113), an endostela containing radially elongate cells (156), and a tracheidal exotegmen (Corner, 1976; 157).

*Caryophyllidae* s.l. Albert et al. (1992) found an unexpected grouping of Droseraceae and Nepenthaceae with Caryophyllales; the latter have been considered to have no particularly close relatives, other than perhaps Plumbaginaceae and Polygonaceae (Cronquist, 1981). This clade appears in all trees, even non-molecular, with a remarkably similar composition (Figs. 2B, 3A, 4A). Most taxa of the clade formed by Rhabdodendraceae (1), Caryophyllales (2), Tamaricaceae (3), Frankeniaceae (4), Asteropeiaceae (5), Nepenthaceae (6), Droseraceae (7), Dioncophyllaceae (8), Ancistrocladaceae (9), Simmondsiaceae (10), Plumbaginaceae (11), and Polygonaceae (12), here termed as caryophyllids, have some taxa with trilcolpate or polycolpate (stephanocolpate) pollen grains (2, 3, 4, 5, 7, 8, 9, 10, 11, 12; Erdtman, 1952; Cronquist, 1981; 129). Many (2, 5, 6, 7, 8, 9, 10, 11, 12) also have spinuliferous or punctitegillate pollen sexine (Erdtman, 1952; 135). The

similarity of pollen grains of some Polygonaceae and some Caryophyllales was noted by Erdtman (1952). Likewise the resemblance of pollen of Droseraceae and Nepenthaceae is noteworthy (e.g., Erdtman, 1952; Basak & Subramanyam, 1966; Takahashi & Sohma, 1982). Anomalous secondary growth seems to be particularly well represented in the caryophyllids, occurring in Rhabdodendraceae, Caryophyllales, Frankeniaceae, Dioncophyllaceae, Simmondsiaceae, and Plumbaginaceae (Carlquist, 1988a). Similarly, interxylary phloem occurs in several taxa: Rhabdodendraceae (Record, 1933), Caryophyllales, Simmondsiaceae (Bailey, 1980), Plumbaginaceae, and Polygonaceae. A character-state that was coded as present in only seven taxa outside the extended caryophyllids is the presence of maximally biseriate wood rays, displayed in Frankeniaceae, Asteropeiaceae, Dioncophyllaceae, Ancistrocladaceae, Droseraceae, and Simmondsiaceae (Metcalfe & Chalk, 1950; Carlquist, 1988a; Carlquist & Wilson, 1995).

The caryophyllids, except for Rhabdodendraceae, are further characterized by the presence of only alternate intervessel pitting (secondary xylem present in 2, 3, 4, 5, 7, 8, 9, 10, 11, 12; 184). The exclusive occurrence of the alkaloid ancistrocladine in Amaranthaceae (Arora & Metha, 1981; 85), Dioncophyllaceae, and Ancistrocladaceae (Hegnauer, 1962–1994) also suggests a degree of relatedness. All caryophyllid families for which information was available (3, 4, 6, 7, 9, 11, 12) have an endosperm provided with starch grains (161); only ten other taxa in the matrix share this condition. Tamaricaceae were previously put into the “Nelken-gruppe,” roughly corresponding to modern concepts of Caryophyllales, by Hallier (e.g., 1914). A tendency linking Tamaricaceae and Frankeniaceae is the presence of exotestal cells with convex surfaces, being represented as papillae in Frankeniaceae or as hairs in Tamaricaceae. Netolitzky (1926) mentioned that the chalazal hair tuft in Tamaricaceae is first developed as papillae. Corner (1976) also postulated a link of Frankeniaceae to Tamaricaceae through exotestal morphology. Moreover, Tamaricaceae as well as Frankeniaceae have appendages on the ventral side of their petals. Airy Shaw (1951) suggested a close affinity of Droseraceae, Nepenthaceae, Ancistrocladaceae, and Dioncophyllaceae. Schmid (1964) added new evidence for this grouping. The latter alignment, containing three carnivorous families (Droseraceae, Nepenthaceae, and Dioncophyllaceae) with different trapping systems, has been supported by Hegnauer (1962–1994) on biochemical grounds.

The presence of the naphthoquinones plumba-

gine (99), droserone (100), and related 1,4-naphthoquinones is another link between Nepenthaceae, Droseraceae, Ancistrocladaceae, Dioncophyllaceae, and Plumbaginaceae (Hegnauer, 1962–1994; Zenk et al., 1969; Durand & Zenk, 1974; Lavault & Bruneton, 1980; Williams et al., 1994); these compounds are otherwise known to be accumulated only by several species of *Fridaceae* and *Ebenaceae* (Hegnauer, 1962–1994).

It is mainly the coincidence of these trends in chemistry and pollen morphology that places the families mentioned above into the expanded caryophyllid clade in the non-molecular tree. Thus, it is the coding of the presence of variably exhibited specialized traits that is responsible for the presence of the caryophyllid clade in nearly the same composition as in the *rbcl* trees. *Rhabdodendraceae*, which fall into the asterids in the non-molecular trees (Fig. 2A), presumably do so because they have unitegmic ovules (see below); with the weak support (69%) present in the *rbcl* data for the expanded caryophyllids, *Rhabdodendraceae* move into this clade in the combined tree.

One of the remarkable aspects of the caryophyllid clade is the diversity of life history strategies that is found among these taxa. Many of these taxa are adapted to either xeric or saline conditions, and some (i.e., *Plumbaginaceae*, *Frankeniaceae*, and *Tamaricaceae*) have multicellular glands that excrete salt (Hill & Hill, 1976; character not coded), whereas others such as *Droseraceae*, have similar glands that produce mucilage and enzymes used to trap and digest insects (Juniper et al., 1989).

A similar *Caryophyllidae* s.l. was also inferred from 18S rDNA data (Soltis et al., 1997b). Comparing the present non-molecular, *rbcl*, and combined trees, the caryophyllids appear in no consistent position with respect to the rosids or asterids. Future combined studies may establish the interrelationships of these clades.

*Asteridae* s.l. The larger asterid clade found with *rbcl* (Olmstead et al., 1992, 1993; Chase et al., 1993; Savolainen et al., 1994; Soltis et al., 1997b) has been remarkably consistent in composition as well as in the general patterns of relationships. This same grouping is present in the non-molecular trees (Fig. 2A), except that some unexpected taxa have additionally been placed here (i.e., *Gunneraceae*, *Sabiaceae*, *Rhabdodendraceae*, and *Santalales*), presumably because these are highly autapomorphic (e.g., *Gunneraceae*) or they have unitegmic ovules like asterids (e.g., *Sabiaceae*, *Rhabdodendraceae*). The absence of these groups from the asterids with *rbcl* analysis can be

interpreted as meaning that the distribution of unitegmic ovules shows some degree of homoplasy. The presence of unitegmic ovules is a consistent character-state in most asterid clades. In a clade corresponding to asterid I, II, and IV of Chase et al. (1993), most taxa have unitegmic ovules (*Hydrangeaceae*, *Cornales*, *Oncothecaceae*, *Sphenostemonaceae*–*Aquifoliaceae*, *Icacinaceae*, *Eucomiales*, *Dipsacales*, *Campanulales*, *Solanales*, *Gentianales*, *Scrophulariales*, *Escalloniaceae*, *Pittosporaceae*, *Araliales*, *Menyanthaceae*, and *Loasaceae*; 137). In addition to characters correlated to some degree with unitegmic and tenuinucellar ovules (137, 139; the correlation including the presence of an integumentary tapetum and endosperm haustoria), the asterids also have a higher percentage of taxa with united sepals (215), and especially with united petals (217), than rosids; this is much more evident than in the more restricted definition of asterids by either Cronquist (1981) or Takhtajan (1987). *Caricaceae* are the only rosid family in this analysis in which all genera have united petals (best developed in the male flowers). In addition to the tendency for the union of perianth whorls, asterids show a higher degree of haplostemony than rosids, a character that is perhaps functionally linked to the more synorganized perianth/androecium. The core asterids (sensu Cronquist, 1981), *Solanales*, *Campanulales*, *Gentianales*, and *Scrophulariales*, are held together by alternate vessel side-wall pitting (184), simple vessel perforations (185), and rounded vessel transverse section (Metcalf & Chalk, 1950; 187).

*Loasaceae* and *Hydrangeaceae* both show the presence of deutzioside (Bliss et al., 1968; Uesato et al., 1986), an iridoid compound known only from these two families (Hegnauer, 1962–1994). Other *rbcl* studies (Soltis et al., 1995a) demonstrated that these two families are sister taxa (but an *rbcl* sequence for *Loasaceae* was unavailable for the present study). Iridoid compounds occur in 19 taxa in our matrix, 16 of which belong to the extended asterids. Light-colored, obdurate, protruding, non-glandular leaf teeth characterize different taxa of *Hydrangeaceae* (character not coded; O. Nandi, pers. obs.). The investigation of leaf teeth in the sister groups of *Hydrangeaceae* is potentially interesting. *Hydrangeaceae* and *Cornales* share the tendency to form inflorescences with showy, sometimes white leafy organs at their periphery. In *Cornales* (*Cornus* spp., *Davidia*) these organs are large bracts, differing only slightly from normal foliage leaves. In *Hydrangeaceae* these organs are the sepals (genera of *Hydrangeaceae*; Engler, 1891). This tendency has not been coded in our matrix (the



organs involved are not homologous). The synorganization of flowers into pseudanthia is a recurring phenomenon in asterids IV and II (sensu Chase et al., 1993; character not used in this analysis).

Taxa having iridoid compounds that are not included in asterids s. str. (sensu Cronquist, 1981) are Hydrangeaceae, Cornales, Icacinaeae, Eucommiales, Escalloniaceae, Loasaceae, Fouquieriaceae, Symplocaceae, Ericales, Sarraceniaceae, and Actinidiaceae (Hegnauer, 1962–1994). These are all asterids in the *rbcl* and combined trees (Figs. 3A, 4A), and also, with one exception, in the non-molecular tree (Fig. 2A).

The presence of a theoid exotesta (152), i.e., an exotesta with lignified and often pitted radial and inner walls (cf. Huber, 1991), links some asterid taxa: Sphenostemonaceae–Aquifoliaceae (*Ilex*; Corner, 1976), Solanales (Solanaceae, e.g., *Atropa*, *Browallia*, *Cestrum*, *Lycium*, *Mandragora*, *Nicandra*, *Nicotiana*, *Petunia*, *Solanum* p.p. *Withania*; Corner, 1976), Dipsacales (Caprifoliaceae, e.g., *Lonicera*; Corner, 1976), Gentianales (Loganiaceae, e.g., *Strychnos*, Gentianaceae, e.g., *Fagraea*; Corner, 1976), Pentaphylacaceae (*Pentaphylax*; Huber, 1991), Marcgraviaceae (*Souroubea*; Huber, 1991), Symplocaceae (*Symplocos*; Huber, 1991), Diapensiaceae (*Diapensia*; Netolitzky, 1926), Ericales (Empetraceae, e.g., *Corema*; Huber, 1991), Sarraceniaceae (Corner, 1976), Clethraceae (Corner, 1976), Actinidiaceae, slightly differentiated in *Saurauia* (Corner, 1976), and Theaceae (Adinandreae; Corner, 1976).

The occurrence of cantleyoside (48), an ester of the iridoid glucoside loganin with the secoiridoid glucoside secologanic acid, is restricted to a few taxa of the asterids II (sensu Chase et al., 1993). This compound is known only from Icacinaeae, Dipsacales, and Campanulales (Hegnauer, 1962–1994; Sévenet et al., 1971; Jensen et al., 1979; Murai et al., 1985; Harborne & Baxter, 1993). The lignan eucommin A (53) is only known from Eucommiales and Gentianales, a fact that supports the placement of Eucommiales in the asterid I clade (sensu Chase et al., 1993; Hegnauer, 1962–1994; Deyama et al., 1985; Harborne & Baxter, 1993).

Oxalate druses (Metcalf, 1950) are absent from the clade formed by Balsaminaceae (1), Pentaphylacaceae (2; no *rbcl* data), Marcgraviaceae (3), Pellicieraceae (4), and Tetrameristaceae (5). All but Pentaphylacaceae have the trait of forming oxalate raphides (1, 3, 4, 5), which is unusual for dicots. A subclade of asterid III (sensu Chase et al., 1993) has a persisting free-central column in loculicidal capsules: Ericales (Ericaceae, Epacridaceae; Drude, 1891b, c; Clethraceae; Drude, 1891a); and Thea-

ceae (Cronquist, 1981; 252). Ericales and Sarraceniaceae are linked by the presence of protruding diffuse placentae. Scytopetalaceae and Lecythidaceae share stratified phloem (Metcalf & Chalk, 1950), cortical vascular bundles (Metcalf & Chalk, 1950), and a nectary disk in the flowers (Scytopetalaceae, Letouzey, 1961; Lecythidaceae subfam. Planchonioidae, Endress, 1994a).

*Rosidae.* Relatively minute embryos (compared to seed size) seem more frequent in the first-branching dicots (magnoliids, hamamelids, some of the first-branching asterids) than in the more nested clades such as Caryophyllidae s.l. and Rosidae. Only 4 out of 74 rosid taxa for which the character has been coded exhibit minute embryos (163): Paeoniaceae, Saxifragales s. str. (in our study, Saxifragales s. str. include Grossulariaceae, Haloragaceae, Penthoraceae, Saxifragaceae; without Vahliaaceae, Greyiaceae, Francoaceae, Parnassiaceae, and Lepuropetalaceae; cf. Takhtajan, 1987), Peridiscaceae, and Tremandraceae. A possible synonymy of Paeoniaceae and Saxifragales s. str. is the presence of an exotestal palisade with thickened outer walls (151) in seeds of *Paeonia* and *Ribes* (Netolitzky, 1926; Corner, 1976). The ridges formed by radial elongation of the exotestal cells in certain Saxifragaceae (similar also in Crassulaceae), according to Corner (1976), "suggest the vestige of a uniformly palisade-like exotesta" in this family. For an extensive study of the Saxifragaceae s.l. and suggestions on their naming see Soltis and Soltis (1997).

Another unexpected grouping in the *rbcl* tree by Chase et al. (1993) is supported in the combined tree. Vochysiaceae/Myrtales (97% bootstrap) have methylated ellagic acids (62), intraxylary phloem (171), vested pits in vessels (Bailey, 1933; van Vliet & Baas, 1984; Carlquist, 1988a; 183), and unilacunar nodes (Cronquist, 1981; Dahlgren & Thorne, 1984; 190).

Tropaecolaceae, Akaniaceae, and Bretschneideraceae, in addition to their glucosinolate production (36), are linked by tricarpelly (233–235). Caricaceae, Capparales, and Salvadoraceae, three glucosinolate-producing taxa, each contain taxa with a fibrous exotegmen (Corner, 1976). Capparales and Salvadoraceae concur in the presence of intra- or interxylary phloem (Carlquist, 1988a; character partially represented in 171). The presence of a single crystal layer (with one oxalate crystal per cell) in the endotesta in Caricaceae (Corner, 1976) and some Capparales (Resedaceae; Corner, 1976) could be a further argument for their affiliation (155). The glucosinolate clade is also present in the

18S rDNA trees (Soltis et al., 1997b) and *atpB* trees (unpublished).

In Malvales s.l., all families have only simple perforations in the secondary xylem (Metcalfe & Chalk, 1950; 185), and all but two families, Cistaceae and Bixaceae, have representatives with mucilage cells or mucilage cavities (Metcalfe & Chalk, 1950; Cronquist, 1981; 119). All taxa for which the character is known (i.e., all except Sarcocaulaceae and Sphaerosepalaceae) are characterized by the occurrence of centrifugal or rarely (Thymelaeaceae; Heinig, 1951) lateral polyandry (Hirmer, 1918; Gore, 1935; Corner, 1946; Van Heel, 1966; Sattler, 1973; Woon & Keng, 1979; Cronquist, 1981; Ronse Decraene, 1989, 1992; Bayer & Hoppe, 1990; Nandi, 1998b; 224). Another synapomorphic character complex for the extended Malvales can be found in seed anatomy. All families for which information is available have representatives with the exotegmen differentiated as a palisade layer (Thymelaeaceae, Sphaerosepalaceae, Malvales s. str., Cochlospermaceae, Bixaceae, Cistaceae, Dipterocarpaceae, and Sarcocaulaceae; Corner, 1976; Nandi, 1998a; 157). An exotegmic palisade occurs only rarely outside of this group (e.g., Trochodendrales, Huaceae, and Euphorbioideae). Malvales s.l. are also linked by the presence of wedge-shaped phloem rays in Thymelaeaceae, Sphaerosepalaceae, Malvales s. str., Cochlospermaceae, and Bixaceae (unknown for Sarcocaulaceae; 170). Moreover, most representatives of Malvales s.l. (except Thymelaeaceae) display a stratified phloem (Metcalfe & Chalk, 1950), a character-state known from just 19 other taxa in this analysis.

Sarcocaulaceae (1), Malvales s. str. (2), Cochlospermaceae (3), Cistaceae (4), Dipterocarpaceae (5), and Bixaceae (6) share the presence of stellate hairs (in 2, 4, 5, 6) and peltate scales (in 1, 2, 3, 4, 5, 6; Metcalfe & Chalk, 1988). This group is also characterized by palmate leaf venation (in Tiliaceae, Sterculiaceae, Bombacaceae, Malvaceae, Cochlospermaceae, Bixaceae, and some *Cistus* species; 198) and frequent tri carpel (233–235). Cochlospermaceae, Bixaceae, Cistaceae, Dipterocarpaceae, and Sarcocaulaceae show the presence of a bixoid chalazal region in the seed (Nandi, 1998a; definition see Appendix 4; 159) as a non-parallelized apomorphy. Moreover, the group is characterized by the absence of a nectary disk (231), and by parietal placentation (241), and large, curved embryos [Cochlospermaceae, Bixaceae, Cistaceae, Dipterocarpaceae (Pakaraimaioideae, Dipterocarpoideae) have large, curved embryos; Janchen, 1925; Pilger, 1925a, b; Maguire & Ashton, 1980; Cronquist, 1981; Nandi, 1998a)]. Vested

pits are found in many representatives of the group [*Bixa* (Solereider, 1899), *Cistus*, Dipterocarpaceae (Monotoideae: Baas & Werker, 1981; Pakaraimaioideae, Dipterocarpoideae), Sarcocaulaceae (Morton, 1995), not in *Cochlospermum*; O. Nandi, pers. obs.; 183]. Cistaceae, Dipterocarpaceae, and Bixaceae share the absence of prodelphinidins (60). Bixaceae and Cistaceae share a starchy endosperm (161) with similar structure of larger starch grains (character not coded; Nandi, 1998a). As in the expanded caryophyllids, it is again a set of specialized character-states that establishes the pattern in the non-molecular trees that then parallels the pattern seen in the *rbcL* trees for the same taxa.

Another unexpected clade, identified in the 1993 *rbcL* trees, was an expanded Malpighiales clade that included families such as Euphorbiaceae, Passifloraceae, Ochnaceae, and Violaceae. This clade is also present in our *rbcL* and combined analyses (Figs. 3B, 4B). Many of these taxa have a fibrous exotegmen (157). Together with the three taxa in the mustard-oil group, this assemblage accounts for 19 of 24 taxa exhibiting a fibrous exotegmen: Connaraceae, Oxalidaceae, and Elaeocarpaceae in Cunoniales; Celastrales s. str.; and Irvingiaceae, Euphorbiales (Phyllanthoideae sensu Corner, 1976), Violaceae, probably Kiggelariaceae, Flacourtiaceae s. str., Scyphostegiaceae, Erythroxylaceae, Malpighiaceae, Linales s. str., Ochnaceae (Sauvagesioideae), Medusagynaceae, and Trigonaceae (Corner, 1976; probable indication of the character for *Medusagyne* by Dickson, 1990). A fibrous exotegmen was also recently described from Rhizophoraceae (*Crossostylis*; Setoguchi et al., 1992), supporting the alliance of this family with rosids having fibrous exotegmen (Malpighiales) and not with Theaceae, as suggested by the non-molecular trees (we became aware of this publication too late to include the character in the matrix). Conti et al. (1996) produced *rbcL* trees that showed Rhizophoraceae and Erythroxylaceae have tropane alkaloids (character not coded). This alkaloid class is otherwise known only in dicots from Proteaceae, Convolvulaceae, Solanaceae, *Cochlearia* (Brassicaceae), and Elaeocarpaceae. The related hygroline alkaloids are confined to Rhizophoraceae and Erythroxylaceae and are known to occur in only two other families [Solanaceae, Brassicaceae (*Cochlearia*); Hegnauer, 1962–1994].

With present knowledge, hostplants of the butterfly genus *Cymothoe* (Nymphalidae: Limenitinae) include only taxa from a few families near Violaceae (character not used in computation); these

families are Clusiaceae, Euphorbiaceae, Dichapetalaceae, Violaceae, Kiggelariaceae, and Flacourtiaceae s. str. (Ackery, 1988). This is one of the rare non-molecular patterns linking Clusiaceae to Euphorbiaceae, and both to Flacourtiaceae.

Violaceae, Kiggelariaceae, Flacourtiaceae s. str., and Scyphostegiaceae are linked by the presence of septate fibers (Metcalfe, 1956; Miller, 1975; 176). The clade formed by Salicaceae, Flacourtiaceae s. str., and Kiggelariaceae has thin wood-fiber walls (Appendix 4; Metcalfe & Chalk, 1950; Miller, 1975; 175), lack of calyx-corolla differentiation (210), absence of alignment of the carpels with the median tepals or petals (232), and loculicidal capsules (251). The close alliance of Salicaceae to Flacourtiaceae s. str. is further suggested by the lepidopteran genus *Cupha* (Nymphalidae: Argynniinae) feeding exclusively on this group (on *Hydnocarpus*, Kiggelariaceae; *Homalium*, *Xylosma*, *Scolopia*, Flacourtiaceae s. str.; and on *Salix*, Salicaceae; Ackery, 1988). Another argynnine genus (*Phalanta*; Ackery, 1988) feeds mainly on *Rinorea*, *Meliccytus*, *Viola* (Violaceae), *Dovyalis*, *Flacourtia*, *Scolopia*, *Trimeria*, *Xylosma* (Flacourtiaceae s. str.), *Rawsonia* (Kiggelariaceae), *Populus*, *Salix* (Salicaceae), and *Maytenus* (Celastraceae). In addition, both Flacourtiaceae s. str. (*Xylosma*, *Poliiothyrsis*) and Salicaceae (*Populus*) have representatives containing the phenolglucoside nigracin, not known from any other family (Hegnauer, 1962–1994; Thiem & Benecke, 1966, 1970; 95). Flacourtiaceae s. str. and Kiggelariaceae, two somewhat preliminary taxa derived from the traditional Flacourtiaceae (e.g., Takhtajan, 1966; Cronquist, 1981), are linked by the presence of finely reticulate pollen ectexine (Keating, 1975; 136), a fibrous exotegmen (in *Casearia*, *Flacourtia* of Flacourtiaceae s. str.; in *Oncoba*, uncertain position, probably Flacourtiaceae s. str.; probably also in *Hydnocarpus*, Kiggelariaceae; Corner, 1976; 157), a hypostase in the seeds (160), septate fibers in the overwhelming majority of genera (Miller, 1975; 176), opposite in addition to alternate vessel side-wall pitting in the wood of the anatomically most basal representatives (*Erythrosperrum*, *Carpotroche*, *Mayna*, *Hydnocarpus*, Kiggelariaceae; *Azara*, Flacourtiaceae s. str.; Miller, 1975; 184), scalariform vessel perforation plates in some representatives (185), and epidermal leaf crystals (196). Within the Flacourtiaceae s. str./Kiggelariaceae assemblage, there seems to be a negative correlation between genera bearing cyanogenic glycosides of the gynocardin type (49) and the genera displaying salicoid teeth (sensu Hickey & Wolfe, 1975; Appendix 4; 201). The two characters seemingly never occur together in the same genus.

In addition to the genera described to have salicoid teeth (*Idesia*, *Populus*, *Salix* in Hickey & Wolfe, 1975; *Prockia* in Morawetz, 1981), twelve other genera from the tribes Homalieae, Scolopieae, Prockieae, and Flacourtieae (sensu Lemke, 1988) have been found to contain species with salicoid teeth: *Dissomeria*, *Byrsanthus*, *Calantica*, *Carriera*, *Flacourtia*, *Homalium*, *Ludia* (not well developed), *Oncoba* (in *Oncobeae* in the system of Lemke, 1988), *Poliiothyrsis*, *Scolopia*, *Trimeria*, and *Xylosma* (O. Nandi, pers. obs.). A broad survey of angiosperm leaves in the herbaria of Zürich (Z and ZT), Geneva (G), and Vienna (WU) indicated that salicoid leaf dentation is a good systematic marker, and that similar tooth types occur only rarely outside of Flacourtiaceae s. str. and Salicaceae (O. Nandi, pers. obs.; e.g., *Tetracentron*). The fact that *Oncoba* lacks both gynocardin-like compounds and has salicoid teeth in addition to glands on the distal end of the petioles (also found in some of the genera with salicoid teeth) indicates that this genus is not well placed among the tribe *Oncobeae* (the definition of the tribe is based on floral morphology following Warburg, 1894). The tribe *Casearieae* (sensu Lemke, 1988) lacks both gynocardin-like compounds and salicoid teeth. Moreover, the two closely related butterfly genera *Siderone* and *Zaretis* (Nymphalidae: Charaxinae: *Anaeini*), are known to feed nearly exclusively on members of this tribe (*Casearia*, *Laetia*, *Ryania*, and *Zuelania*; Ackery, 1988). Other genera of the subtribe *Anaeini* feed mainly on Euphorbiaceae. This pattern could indicate that *Casearieae* are not immediately connected to other tribes of Flacourtiaceae s.l. Conversely, the genus *Cymothoë*, mentioned previously, feeds on *Casearia* (*Casearieae*), *Rausonia* (*Erythrospermeae*), *Buchnerodendron*, *Caloncoba* (*Oncobeae*), *Kiggelaria* (*Pangieae*), and *Dovyalis* (*Flacourtieae*), as well as on Clusiaceae, Euphorbiaceae, and Dichapetalaceae (Ackery, 1988). A relationship of Kiggelariaceae to Passiflorales is suggested by the fact that at least three butterfly species of *Acraea* subg. *Acraea* (Nymphalidae: *Acraeinae*: sensu Pierre, 1984) feed on Kiggelariaceae, and Passifloraceae tribes *Paropsieae* (no molecular data available) and *Passifloreae* (an extrinsic character, not in the matrix). The first molecular insights into Flacourtiaceae s.l. using *rbcl* sequence data information were provided in Chase et al. (1996); a great deal more study of this and related families will be required to establish proper family circumscriptions.

A relationship of Violaceae to the flacourtiaceous line is further indicated by the hostplants of *Acraea cerasa*, found to be an early-branching representa-

tive of the subgenus *Acraea* in a morphological cladistic study by Pierre (1984). This species is known to feed on both *Rinorea* (Violaceae) and *Rausonia* (Kiggelariaceae). Other species of subgenus *Acraea* feed exclusively on Violaceae and Passiflorales. *Acraea* subg. *Acraea* thus seems to show loose co-evolutionary correlations with representatives of Violaceae, Flacourtiaceae s. str., Kiggelariaceae, Passifloraceae, and Tumeraceae.

Linales s. str., Passiflorales, and Euphorbiales also share the exclusive capacity of producing the cyanogenic diglucosides linustatin and neolinustatin (character-states not included in the matrix for Euphorbiales; 29, 30). The two compounds are transport-forms of the widely distributed monoglucosylated cyanogenes linamarin and lotaustralin (Hegnauer, 1962–1994; Smith et al., 1980; Selmar, 1993; Frehner et al., 1990; Mkpog et al., 1990). They are formed during seed development (*Linum*), seed germination (*Hevea*), or tuber formation (*Manihot*).

Quinaceae, Ochnaceae, and Medusagynaceae have at least some taxa with contorted petal aestivation (*Touroulia*, Quinaceae, Engler, 1925; Ochnaceae, Gilg, 1925; Medusagynaceae, Engler & Melchior, 1925). Links of Ochnaceae to Medusagynaceae can be seen in the common presence of stratified phloem (known for *Godoya* in Ochnaceae and Medusagynaceae, Metcalfe & Chalk, 1950), cortical vascular bundles in the stem, septical capsules, and a persistent free-central column in the fruits (Fay et al., 1997).

Connaraceae and Oxalidaceae (here in Cunoniaceae; Figs. 3B, 4B) share the absence of ellagic acid and the presence of rapanone, a benzoquinone (Fieser & Chamberlain, 1948; Hegnauer, 1962–1994). Rapanone is only known from a few angiosperm families, including Myrsinaceae, according to Hegnauer (1962–1994). Connaraceae and Oxalidaceae are further linked on the basis of sieve-tube plastids of the Plc-type (Behnke, 1981; 107), the absence of oxalate druses (Metcalfe & Chalk, 1950; 112), a short exostetal palisade [Connaraceae (*Cnestis*, *Connarus* spp., *Jollydora*, *Rourea*), Oxalidaceae (*Averrhoa*); Corner, 1976; 151], endostetal crystals [Connaraceae (*Jollydora*), Oxalidaceae (*Averrhoa*, *Oxalis*); Corner, 1976; 155], fibrous exotegmen [Connaraceae (*Cnestis*, *Jollydora*, *Rourea*), Oxalidaceae (*Averrhoa*, *Oxalis*); Corner, 1976; 157], and exclusively uniseriate wood rays (181).

Celastrales s. str. and Plagiopteraceae are linked by the common presence of epidermal crystals in the leaves (Baas et al., 1979; 196), the occurrence of weakly crassinucellar ovules in representatives of both taxa (*Celastrus* and *Cassine* (as *Elaeoden-*

*dron*), Celastrales s. str., Johri et al., 1992; *Plagiopteron*, Tang, 1994; 139), and an integumentary tapetum (Johri et al., 1992; Tang, 1994; 138).

Cephalotaceae, Eucryphiaceae, Brunelliaceae, and Cunoniaceae all have representatives with follicles or ventricidal capsules (Engler, 1930; Bausch, 1938; Cronquist, 1981; 251), and Brunelliaceae and Cunoniaceae have opposite leaves (191) with frequently craspedodromous venation (O. Nandi, pers. obs.; 199). A similar Cunonioid clade was found in the 18S rDNA trees (Soltis et al., 1997b).

The taxa with nitrogen-fixing root symbionts in at least some genera [Fabaceae, Cucurbitales (Datisceae), Coriariaceae, Faganae (Myricaceae, Betulaceae, Casuarinaceae), Rosaceae, Rhamnaceae, Urtales (Ulmaceae), and Elaeagnaceae; 105], with the exception of Fabaceae, are placed in a monophyletic clade in the combined tree. In the *rbcl* trees (Fig. 3B), Fabaceae are also members of this clade, but they are placed outside the clade in the combined tree (Fig. 4B). Fabaceae, Myricaceae, Betulaceae, Casuarinaceae, Ulmaceae, and Elaeagnaceae are known to contain nodule hemoglobin (Landsmann et al., 1986; this character was not used in the non-molecular matrix). The hostplant taxa of the hyphomycete *Tubercularia ulmea* [Rhamnaceae (*Rhamnus*), Elaeagnaceae (*Elaeagnus*), Urtales (*Ulmus*); Farr et al., 1989] form a monophyletic clade in the trees derived from the combined data set, a fact that could point to a co-evolutionary relationship of the fungus and these rosids. In both the 18S (Soltis et al., 1997b) and *atpB* trees (Savolainen et al., 1996), this same nitrogen-fixing clade is present.

There are many other specific characteristics upon which some discussion could be made, but at this point in time, this is not appropriate. We have focused in the previous section on features that are of particular interest to us. The most significant outcome of these comparisons is that chemical and micromorphological (often palynological) data should be included as equally important characters as developmental and floral morphological traits in macrosystematic considerations. These characters seem to correspond most closely to the molecular results. Gross morphological traits, particularly phyllotaxy, presence of stipules, and perianth arrangement, appear especially unreliable for systematic interpretations at this level within angiosperms.

(C) TAXA FOR WHICH *rbcl* SEQUENCES ARE NOT AVAILABLE

Hydnoraceae (not included in our matrices) have been allied to Aristolochiales in some systems (e.g.,

Takhtajan, 1987). Characters of Hydnoraceae tending to be ancestral are monosulcate, di- or trisulcate as well as trichotomocolpate pollen (x-tomocolpate pollen known in Chloranthaceae, *Cabomba*, Saururaceae, and monocots), psilate exine, thick endexine as compared to the ectexine, unitegmic, orthotropous ovules (as in Ceratophyllaceae, but probably also correlated with the high ovule number and parasitism), a well developed perisperm (a character more widespread in basal than in advanced angiosperms), a minute embryo in the seed, non-arborescent growth form, and a perianth not differentiated into calyx and corolla.

Rafflesiaceae (not included in our matrices) are known to be heterogeneous both in pollen characters and macromorphology (Takhtajan et al., 1985). It is possible that the different families recognized by Takhtajan (1987), i.e., Rafflesiaceae s. str., Apodanthaceae, Mitrastemonaceae, and Cytinaceae, belong to distantly related groups. The occurrence of ellagitannins (characteristic for eudicots) and 2-, 3-, or 4-porate pollen grains in *Cytinus* and the tricolpate pollen grains in *Pilostyles* suggest the absence of a close relationship to *Rafflesia*, *Rhizanthus*, and *Sapria*, which have monosulcate or monoporate pollen (the recent 18S rRNA information on Rafflesiales by Nickrent, 1996, confirms the segregation of *Cytinus* from Rafflesiaceae s. str.). The occurrence of both a lamellate endexine and an atectate ectexine in the pollen of Rafflesiaceae s. str. (Takhtajan et al., 1985) is likely an ancestral character combination for angiosperms.

In the fossil record, epigynous angiosperm flowers from the Early Cretaceous of Portugal have been found (Friis et al., 1994). Partly, these flowers are of unclear systematic affinity; some of them have similarities with Laurales. In extant basal angiosperms epigynous flowers are comparatively rare, although they are present in several families. The fact that Hydnoraceae and Rafflesiaceae s. str. have epigynous flowers and the seemingly ancestral characters found in these two families call for their integration in the research on first-branching angiosperms. It would be especially interesting to include them in molecular systematic studies, because morphological and anatomical characters are difficult to assess (because of reductions due to parasitism). Analysis of 18S rDNA sequences would be the most likely source of useful information to address questions about these parasitic plants, but the high levels of divergence for these plants (Nickrent, 1996) coupled with the low levels of divergence for 18S rDNA found in angiosperms in general (Soltis et al., 1997b) are likely to make sequence evaluations unreliable.

Podostemaceae are another family with unusual biology for angiosperms in general, and are thus difficult to assess. In our non-molecular trees, they generally fall near or in the Caryophyllids or less frequently Santalales. Despite rather incomplete data, character-states of systematic importance are the occurrence of silica bodies (111) and secretory cavities in the plant body, tricolpate pollen grains with spinulose exine and colpus membrane (Rutishauser, 1997; 130, 135), tenuinucellar ovules (139), suspensor haustoria (165), absence of calyx-corralla differentiation (210), rare occurrence of centrifugal androecium development (in *Mourera fluviatilis* Aubl., R. Rutishauser, pers. comm.; 224), prolonged stamen connectives (229), generally completely free styles [except for, e.g., "*Synstylis*" (*Polypleurum*); 237], micropyle formation by the outer integument (247), and septical capsules (251). Some of these characters may be seen as adaptations to the extreme habitat of Podostemaceae. Ueda et al. (1997), using *rbcL* sequence data, found that Podostemaceae are sister to Crassulaceae in the saxifragoid clade. Les and Philbrick (1996) reported extremely high levels of divergence for several Podostemaceae, but also concluded that they are sister to Crassulaceae.

Balanophoraceae are also highly reduced due to their parasitic ecology. They tend to align in extended caryophyllids. Triangular pollen grains (132) and the occurrence of similar embryo sacs could indicate a link to Santalales (Zweifel, 1939). The 18S rRNA analysis of Nickrent (1996) contradicted a close alliance of Balanophoraceae with Santalales. As with Podostemaceae, our matrix for Balanophoraceae has many gaps.

Strasburgeriaceae tend to be placed in basal asterids in the present non-molecular trees. Oncothecaceae are another small family placed in the asterids near Aquifoliaceae. Preliminary *rbcL* analyses support this position for *Oncotheca* (Savolainen & Chase, unpublished). Paracryphiaceae cluster with basal asterids or Eucryphiaceae.

Rhizophoraceae either fall near to the Stachyuraceae group or often are the sister group to Theaceae. Published and unpublished *rbcL* analyses support a placement of Rhizophoraceae in Malpighiales (Conti et al., 1996) near Erythroxylaceae (Chase et al., unpublished). The fibrous exotegmen in Rhizophoraceae, described by Setoguchi et al. (1992), would be in good agreement with the molecular results (see Discussion, section b).

Sarcolaenaceae align with Malvales s.l.; this is also confirmed with recent *rbcL* analyses (Conti et al., 1996). Cochlospermaeae also clearly align with Malvales s.l. as sister to a branch containing

Bixaceae and Cistaceae. Other analyses of *rbcL* also support this placement (Alverson et al., in press).

Bonnetiaceae, Elatinaceae (non-molecular data), and Clusiaceae (also with *rbcL*) are kept together by an exotegmen with lobate facets in tangential section (158). All three families have representatives with septicidal capsules (251). These three taxa are linked in the non-molecular trees. The close relationship of the three families was emphasized by Stevens (1991). Clusiaceae and Bonnetiaceae, in addition, are united by having representatives with arils (perhaps a vestigial aril in *Ploiarium*; Corner, 1976; 146) and protruding diffuse placentation (242). Preliminary *rbcL* studies of *Ploiarium* place it near Thymelaeaceae in Malvales s.l. (Chase, unpublished), but other Bonnetiaceae may not be related to *Ploiarium* (A. Weitzman, pers. comm.).

#### (D) CONCLUSIONS

Larger data matrices call for improved computational facilities, both in tree searches and in assessing confidence in the resulting clades (e.g., jackknife program, Farris et al., 1997). It has been recognized in these searches that the stronger the phylogenetic signal in a matrix, the easier it is to obtain reasonably short trees. In a sense, once one has found all the strongly supported clades, then the search is complete. Regardless of the manner in which weakly supported branches are arranged, there can be no confidence in the patterns so produced. In experiments with combining large *rbcL*, *atpB*, and 18S matrices, it has been noted that tree searches have become faster and production of a reasonably short tree length appears relatively easy (Soltis et al., 1997b; Chase & Savolainen, unpublished). We are optimistic that, as we add more data as well as more taxa, searches will in fact become easier rather than more difficult. Hillis's (1996) recent simulations and predictions also support the notion that increased sampling, both of genes and taxa, produces more accurate topologies; increase in accuracy by sampling more genes has been accepted for some time, whereas it has been a hotly disputed topic whether increased sampling of taxa also produces more reliable topologies (see for example Graur et al., 1996).

On the molecular-systematic side, improved topologies will be obtained by integrating and comparing more sequence-information from different genomes; this should allow us to have more confidence in the relationships obtained and to evaluate whether reticulate evolution through an-

cient hybridization or horizontal gene transfer has macrosystematic effects.

The work on the "classical" side is equally challenging. Cladistic analyses using non-molecular data should rely if possible on original observations of living plants, herbarium material, and anatomical slide collections, but also on primary and synoptic literature. Literature searches ideally should also include the older comparative literature (e.g., works by Baillon, Bentham & Hooker, Eichler, Engler & Prantl, Payer, Troll), which contains much useful and recently overlooked information.

Biochemical work can be refined, and new techniques will doubtless permit more detailed comparison of the different molecule classes. This promises to be a fruitful field, especially for families on which not much biochemical work has been done, such as Ceratophyllaceae, Hydnoraceae, Rafflesiaceae, Amborellaceae, Eupteleaceae, Sabiaceae, Didymelaceae, Aextoxicaceae, Strasburgeriaceae, Sphenostemonaceae, Oncothecaceae, Tetrameristaceae, Pellicieraceae, Pentaphragmataceae, Diapensiaceae, Scytopetalaceae, Dyalypetalanthaceae, Bruniaceae, Plagiopteridaceae, Irvingiaceae, Sphaerosepalaceae, Diegodendraceae, and Sarcolaenaceae.

The study of the form and distribution of solid bodies in cells also reveals additional systematic information (e.g., oxalate crystals, starch grains; preliminary works by Czaja, 1969, 1978). The same holds true for investigations of plant hair structure.

Much more information on seed anatomy should also be sampled. Priorities again are small families of restricted distribution, as mentioned above. Seed anatomy has proven to be a good tool for macrosystematics in the present study (see also Corner, 1976; Huber, 1991; Seubert, 1993).

A character-rich field that has not yet received much attention from neobotanists is leaf structure (see Hickey & Wolfe, 1975; Klucking, 1986/1987/1988/1989/1991/1992/1995). Leaf morphology (leaf dentation, leaf venation patterns) is of great potential usefulness, especially in combination with paleobotany.

Rhizome, bulb, and root morphology and anatomy are presently not as well understood as, e.g., floral morphology. Floral ontogeny is a field in which new perspectives have been achieved by the use of SEM (e.g., Endress, 1994a; Tucker & Douglas, 1994; Erbar & Leins, 1996). Because of practical problems in acquiring different ontogenetic stages, there are still many groups that remain poorly known. Inflorescence types have been studied for many families and are likely to be valuable for phylogenetic analyses. Fruit anatomy has not

received much attention, probably also due to the large size of many angiosperm fruits. Recent works on Oleales (e.g., Rohwer, 1996) and Cornales (Reidt, 1997) show that comparison of fruit characters is systematically relevant.

As with intrinsic characters of angiosperms, extrinsic ones from fields such as ecology, paleoecology, paleobotany, biogeography, and hostplant and mutualistic relationships should also provide useful data. In the last field, more information should be sampled on hostplants of fungi, Lepidoptera, and other groups of organisms that tend to have taxa with restricted preference for particular angiosperms (perhaps also Orthoptera, Aphididae, and Chrysomelidae). Paleobotany is a promising field for providing insights on early angiosperm radiation and relationships to possible outgroups. It may also add evidence on the position of controversially positioned clades that cannot be assigned clearly to the asterids, rosids, or caryophyllids as described here and in Chase and Cox (in press).

We are optimistic about the prospects for improved analyses of all classes of data. This study provides one example of how this approach can succeed, but a great deal more work on methods of coding characters is needed. In which cases can tendencies be coded as uniform characters for families in which polymorphisms occur? Should a family or order, no matter how clearly supported as monophyletic, be used as a terminal? These results appear to demonstrate that this approach can succeed with both molecular and non-molecular data and that the phylogenetic content of characters so coded is not terribly distorted by this type of summarization. We suspect that, if the patterns are robust, different codings will provide similar results. What is most needed is not a dogmatic approach to character coding and skepticism of the potential for various coding methods to succeed, but an empirical evaluation of real data using consistent methods. Too much emphasis on methodological matters will only serve to impede progress. We maintain that the barriers to creating large matrices and performing analyses on large data sets have less to do with the data collection and analysis than with much skepticism of the process itself.

Literature Cited

Ackery, P. R. 1983. Hostplants and classification: A review of nymphalid butterflies. *Biol. J. Linn. Soc.* 33: 95-203.  
 ———. 1991. Hostplant utilization by African and Australian butterflies. *Biol. J. Linn. Soc.* 42: 335-351.  
 Airy Shaw, H. K. 1951. On the Dioncophyllaceae, a re-

markable new family of flowering plants. *Kew Bull.* 3: 327-347.  
 Albert, V. A., S. E. Williams & M. W. Chase. 1992. Carnivorous plants: Phylogeny and structural evolution. *Systematics* 257: 1491-1495.  
 Aldrich, J., B. Cherney & E. Merlin. 1986. Sequence of the *rbcL* gene for the large subunit of ribulose biphosphate carboxylase-oxygenase from alfalfa. *Nucl. Acids Res.* 14: 9535.  
 Alverson, W. S., K. Karol, E. Conti & J. Sytsma. 1994. Circumscription of the Malvales and its placement in rosids based on *rbcL* sequence data. *Amer. J. Bot.* 81 (Suppl., 6): 139. [Abstract.]  
 ———, D. A. Baum, M. W. Chase, S. M. Swensen, R. McCourt & K. J. Sytsma. Circumscription of the Malvales and relationships to other Rosidae: Evidence from *rbcL* sequence data. *Amer. J. Bot.* (in press).  
 Arber, A. 1925. *Monocotyledons. A Morphological Study.* Cambridge Univ. Press, Cambridge.  
 Arora, O. P. & M. Metha. 1981. Chemical investigations of some Rajasthan desert plants. *Indian J. Chem.*, B 20: 834.  
 Baas, P. 1969. Comparative anatomy of *Platanus kerrii* Gagnep. *Bot. J. Linn. Soc.* 62: 413-422.  
 ———. 1972. Anatomical contributions to plant taxonomy II. The affinities of *Hua Pierre* and *Afrostryax* Perkins et Gilg. *Blumea* 20: 161-192.  
 ———. 1975. Vegetative anatomy and the affinities of Aquifoliaceae, *Sphenostemon*, *Phelline* and *Oncotheca*. *Blumea* 22: 311-407.  
 ———. 1984. Vegetative anatomy and taxonomy of *Berberidopsis* and *Streptothamnus* (Flacourtiaceae). *Blumea* 30: 39-44.  
 ——— & E. Werker. 1981. A new record of vestured pits in Gistaceae. *I.A.W.A. Bull.*, N. S. 2: 41-42.  
 ———, R. Geesink, W. A. Van Heel & J. Muller. 1979. The affinities of *Plagiopteron suaveolens* Griff. (Plagiopteraceae). *Grana* 18: 69-89.  
 Bailey, D. C. 1980. Anomalous growth and vegetative anatomy of *Simmondsia chinensis*. *Amer. J. Bot.* 67: 147-161.  
 Bailey, I. W. 1933. The cambium and its derivative tissues. VIII. Structure, distribution and diagnostic significance of vestured pits in dicotyledons. *J. Arnold Arbor.* 14: 259-273.  
 ———. 1957. Additional notes on the vesselless dicotyledon, *Amborella trichopoda* Baill. *J. Arnold Arbor.* 38: 374-380.  
 ——— & B. G. L. Swamy. 1948. *Amborella trichopoda* Baill. A new morphological type of vesselless dicotyledon. *J. Arnold Arbor.* 29: 245-254.  
 Baillon, H. 1873. *Histoire des Plantes*, Vol. 3. Hachette, Paris.  
 Baretta-Kuipers, T. 1976. Comparative wood anatomy of Bonnetiaceae, Theaceae and Guttiferac. *Leiden Bot. Ser.* 3: 76-101.  
 Barron, D., L. Varin, R. K. Ibrahim, J. B. Harborne & C. A. Williams. 1983. Sulphated flavonoids—An update. *Phytochemistry* 27: 2375-2395.  
 Barth, O. P. 1965. Elektronenmikroskopische Beobachtungen am Sporerderm der Caryocaraceen. *Grana Palynol.* n. s. 6: 7-25.  
 Basak, R. K. & K. Subramanyam. 1966. Pollen grains of some species of *Nepenthes*. *Phytomorphology* 16: 334-338.  
 Batygina, T. B., O. P. Kamelina, A. L. Takhtajan, M. S. Yakovlev & G. Ya. Zhukova. 1985a. Comparative Em-

- biology of the Flowering Plants, Butomaceae–Lemnaceae. Nauka, Leningrad. [In Russian.]
- \_\_\_\_\_, \_\_\_\_\_, & \_\_\_\_\_. 1985b. Comparative Embryology of the Flowering Plants, Brunelliaceae–Tremandraceae. Nauka, Leningrad. [In Russian.]
- \_\_\_\_\_, \_\_\_\_\_, & \_\_\_\_\_. 1985c. Comparative Embryology of the Flowering Plants, Davidiaceae–Asteraceae. Nauka, Leningrad. [In Russian.]
- Bausch, J. 1938. A revision of the Eucryphiaceae. Bull. Misc. Inform. Kew 1938: 317–349.
- Bayer, C. & J. R. Hoppe. 1990. Die Blütenentwicklung von *Theobroma cacao* L. (Sterculiaceae). Beitr. Biol. Pflanzen 65: 301–312.
- Bedell, H. G. 1981. Leaf architecture and foliar sclereids in Marcgraviaceae (Theales). Publ. Bot. Soc. Amer., Misc. Ser. 160: 62.
- Behnke, H.-D. 1975. The bases of angiosperm phylogeny: Ultrastructure. Ann. Missouri Bot. Gard. 62: 647–663.
- \_\_\_\_\_. 1977. Zur Skulptur der Pollen-Exine bei drei Centrospermen (*Gisekia*, *Lineum*, *Hectorella*), bei Gyrostemonaceen und Rhabdodendraceen. Pl. Syst. Evol. 128: 227–235.
- \_\_\_\_\_. 1981. Sieve-element characters. Nordic J. Bot. 1: 381–400.
- \_\_\_\_\_. 1985. Contributions to the knowledge of P-type sieve-element plastids in dicotyledons II: Eucryphiaceae. Taxon 34: 607–610.
- Berg, C. C. 1977. Urticales, their differentiation and systematic position. Pl. Syst. Evol., Suppl. 1: 349–374.
- Beusekom, C. F. van. 1971. Revision of *Meliosma* (Sabiaceae), section *Lorenziana* excepted, living and fossil, geography and phylogeny. Blumea 19: 355–529.
- Bhandari, N. N. 1971. Embryology of the Magnoliales and comments on their relationships. J. Arnold Arbor. 52: 1–39, 285–304.
- Blackmore, S., P. Stafford & V. Persson. 1995. Palynology and systematics of Ranunculiflorae. Pl. Syst. Evol., (Suppl.) 9: 71–82.
- Blank, F. 1939. Beitrag zur Morphologie von *Caryocar nuciferum* L. Ber. Schweiz. Bot. Ges. 49: 437–494.
- Bliss, C. A., T. J. Danielson & R. A. Abramovitch. 1968. Investigations on the genus *Mentzelia*. I. Mentzeloside, a new iridoid glycoside. Lloydia 31: 424.
- Boesewinkel, F. D. 1985. Development of ovule and seed-coat in *Aerhhoa* (Oxalidaceae) with notes on some other related genera. Acta Bot. Neerl. 34: 413–424.
- \_\_\_\_\_. 1994. Ovule and seed characters of *Balanites aegyptiaca* and the classification of the Linales–Geraniales–Polygalales assembly. Acta Bot. Neerl. 43: 15–25.
- \_\_\_\_\_ & F. Bouman. 1980. Development of the ovule and seed-coat of *Dichapetalum mombuttense* Engl. with notes on other species. Acta Bot. Neerl. 29: 103–115.
- Bohm, B. A. & J. Chan. 1992. Flavonoids and affinities of Greyiaceae with discussion of the occurrence of B-ring deoxyflavonoids in dicotyledonous families. Syst. Bot. 17: 272–281.
- Bonreau, E. 1958. Contribution à l'étude des espèces actuelles de Rhopalocarpaceae. Bull. Mus. Hist. Nat. sér. 2. 30: 213–221.
- Brenner, G. J. 1990. An evolutionary model of angiosperm pollen evolution based on fossil angiosperm pollen from the Hauterivian of Israel. Amer. J. Bot. 77 (Suppl., 6): 82. [Abstract.]
- \_\_\_\_\_. 1996. Evidence for the earliest stage of angiosperm pollen evolution: A paleo-equatorial section from Israel. Pp. 91–115 in D. W. Taylor & L. J. Hickey (editors), Flowering Plant Origin, Evolution and Phylogeny. Chapman & Hall, New York.
- Brizicky, G. K. 1964. The genera of Cistaceae in the southeastern United States. J. Arnold Arbor. 45: 346–357.
- Brüning, R. & H. Wagner. 1978. Uebersicht über die Celastraceen-Inhaltsstoffe: Chemie, Chemotaxonomie, Biosynthese, Pharmakologie. Phytochemistry 17: 1821–1858.
- Burger, W. C. 1977. The Piperales and the monocots. Alternative hypotheses for the origin of monocotyledonous flowers. Bot. Rev. (Lancaster) 43: 345–393.
- Canright, J. E. 1955. Comparative morphology and relationships of the Magnoliaceae—IV. Wood and nodal anatomy. J. Arnold Arbor. 36: 119–140.
- Capuron, R. 1974. Une variété nouvelle d'*Asteropeia amblyocarpa* Tul., Théacée de Madagascar. Adansonia n. s. 14: 291–292.
- Carlquist, S. 1964. Pollen morphology and evolution of Sarcocaulaceae (Chlaenaceae). Brittonia 16: 231–254.
- \_\_\_\_\_. 1976. Wood anatomy of *Myrothamnus flabellifolia* (Myrothamnaceae) and the problem of multiperforate perforation plates. J. Arnold Arbor. 119–126.
- \_\_\_\_\_. 1977. Wood anatomy of Tremandraceae: Phylogenetic and ecological implications. Amer. J. Bot. 64: 704–713.
- \_\_\_\_\_. 1981. Wood anatomy of Pittosporaceae. Allertonia 2: 355–391.
- \_\_\_\_\_. 1984a. Wood anatomy of Loasaceae with relation to systematics, habit and ecology. Aliso 10: 583–602.
- \_\_\_\_\_. 1984b. Wood anatomy of Polemoniaceae. Aliso 10: 547–572.
- \_\_\_\_\_. 1984c. Wood anatomy and relationships of Pentaphragmaceae: Significance of vessel features. Phytomorphology 34: 84–90.
- \_\_\_\_\_. 1984d. Wood and stem anatomy of *Bergia suffruticosa*: Relationships of Elatinaceae and broader significance of vascular tracheids, vascentric tracheids, and fibrifrom vessel elements. Ann. Missouri Bot. Gard. 71: 232–242.
- \_\_\_\_\_. 1988a. Comparative Wood Anatomy. Springer, Berlin.
- \_\_\_\_\_. 1988b. Wood anatomy of Scytopetalaceae. Aliso 12: 63–76.
- \_\_\_\_\_. 1990. Wood anatomy and relationships of Lactoridaceae. Amer. J. Bot. 77: 1498–1505.
- \_\_\_\_\_. 1993. Wood anatomy of Sabiaceae (s.l.): Ecological and systematic implications. Aliso 13: 521–549.
- \_\_\_\_\_ & D. A. Hoekman. 1985. Ecological wood anatomy of the woody southern Californian Flora. I.A.W.A. Bull., N. S. 6: 319–347.
- \_\_\_\_\_ & E. J. Wilson. 1995. Wood anatomy of *Drosophyllum* (Droseraceae): Ecological and phylogenetic considerations. Bull. Torrey Bot. Club 122: 185–189.
- Carpenter, C. S. & W. C. Dickison. 1976. The morphology and relationships of *Oncotheca balansae*. Bot. Gaz. 137: 141–153.
- Carpenter, J. M. 1983. Choosing among multiple equally parsimonious cladograms. Cladistics 4: 291–296.
- Chase, M. W. & A. V. Cox. Gene sequences, collaboration, and analysis of large data sets. Austral. Syst. Bot. (in press).
- \_\_\_\_\_ & S. M. Swensen. 1995. Relationships of *Viola* sensu Cronquist from the perspective of cladistic



- analyses of *rbcL* sequence data. *Amer. J. Bot.* 82 (Suppl., 6): 119. [Abstract.]
- , M. D. Lledó, M. B. Crespo & S. M. Swensen. 1996. "When in doubt put it in the Flacourtiaceae": Molecular systematics of Flacourtiaceae. *Amer. J. Bot.* 83 (Suppl., 6): 146. [Abstract.]
- , D. W. Stevenson, P. Wilkin & P. J. Rudall. 1995. Monocot systematics: A combined analysis. Pp. 685–730 in P. J. Rudall, P. J. Cribb, D. F. Cutler & C. J. Humphries (editors), *Monocotyledons: Systematics and Evolution*. Royal Botanic Gardens, Kew.
- , D. E. Soltis, R. G. Olmstead, D. Morgan, D. H. Les, B. D. Mishler, M. R. Duvall, R. A. Price, H. G. Hills, Y.-L. Qiu, K. A. Kron, J. H. Rettig, E. Conti, J. D. Palmer, J. R. Manhart, K. J. Sysma, H. J. Michaels, W. J. Kress, K. G. Karol, W. D. Clark, M. Hedrén, B. S. Gaut, R. K. Jansen, K.-J. Kim, C. F. Wimper, J. F. Smith, G. R. Furnier, S. H. Strauss, Q.-Y. Xiang, G. M. Plunkett, P. S. Soltis, S. Swensen, S. E. Williams, P. A. Gadek, C. J. Quinn, L. E. Eguarte, E. Golenberg, G. H. Learn, Jr., S. W. Graham, S. C. H. Barrett, S. Dayanandan & V. A. Albert. 1993. Phylogenetics of seed plants: An analysis of nucleotide sequences from the plastid gene *rbcL*. *Ann. Missouri Bot. Gard.* 80: 528–580.
- Chiarugi, A. 1925. *Embriologia delle Cistaceae*. *Nuovo Giorn. Bot. Ital.* n.s. 32: 223–314.
- & E. Francini. 1930. *Apomissia in "Ochna serrulata"* Walp. *Nuovo Giorn. Bot. Ital.* n.s. 37: 1–250.
- Chopra, R. N. & K. Harjinder. 1965. Embryology of *Bixa orellana* L. *Phytomorphology* 15: 211–214.
- Conti, E., A. Fischbach & K. J. Sysma. 1993. Tribal relationships in Onagraceae: Implications from *rbcL* sequence data. *Ann. Missouri Bot. Gard.* 80: 672–685.
- , A. Litt & K. J. Sysma. 1996. Circumscription of Myrtales and their relationships to other rosids: Evidence from *rbcL* sequence data. *Amer. J. Bot.* 83: 221–233.
- Cook, C. D. K. 1978. *The Hippuris syndrome*. Pp. 163–176 in H. E. Street (editor), *Essays in Plant Taxonomy*. Academic Press, London.
- Corner, E. J. H. 1946. Centrifugal stamens. *J. Arnold Arb. 27*: 423–437.
- . 1976. *The Seeds of Dicotyledons*, Vols. 1 and 2. Cambridge Univ. Press, Cambridge.
- Crane, P. R. 1989. Paleobotanical evidence of the early radiation of nonmagnoliid dicotyledons. *Pl. Syst. Evol.* 162: 165–191.
- , E. M. Friis & K. R. Pedersen. 1995. The origin and early diversification of angiosperms. *Nature* 374: 27–33.
- , K. R. Pedersen, E. M. Friis & A. N. Drinnan. 1993. Early Cretaceous (Early to middle Albian) platanoid inflorescences associated with *Sapindopsis* leaves from the Potomac group of eastern North America. *Syst. Bot.* 18: 328–344.
- Cronquist, A. 1981. *An Integrated System of Classification of Flowering Plants*. Columbia Univ. Press, New York.
- . 1983. Some realignments in the dicotyledons. *Nordic J. Bot.* 3: 75–83.
- Crossley, N. S. & C. Djerassi. 1962. Naturally occurring oxygen heterocyclics. Part XI. Veraguensin. *J. Chem. Soc.* 1962: 1459–1462.
- Cuatrecasas, J. 1985. Brunelliaceae. *Fl. Neotrop. Monogr.* 2 (Suppl.): 1–189.
- Czaja, A. T. 1969. *Mikroskopie der Stärkekörner*. Parey, Berlin.
- . 1978. *Stärke und Stärkekörner bei Gefäßpflanzen*. Fischer, Stuttgart.
- Dahlgren, R. M. T. 1980. A revised system of classification of angiosperms. *Bot. J. Linn. Soc.* 80: 91–124.
- . 1983. General aspects of angiosperm evolution and macrosystematics. *Nordic J. Bot.* 3: 119–149.
- & H. T. Clifford. 1982. *The Monocotyledons: A Comparative Study*. Academic Press, London.
- & V. S. Rao. 1969. A study of the family Geissolemataceae. *Bot. Not.* 122: 207–227.
- & R. F. Thorne. 1984. The order Myrtales: Circumscription, variation, and relationships. *Ann. Missouri Bot. Gard.* 71: 633–699.
- , H. T. Clifford & P. F. Yeo. 1985. *The Families of the Monocotyledons. Structure, Evolution, and Taxonomy*. Springer, Berlin.
- Davis, G. L. 1966. *Systematic Embryology of the Angiosperms*. Wiley & Sons, New York.
- Dechamps, R. 1979–1985. *Étude anatomique de bois d'Amérique du Sud*, Vols. 1–3. Musée Royal de l'Afrique Centrale, Tervuren.
- Decker, J. M. 1966. Wood anatomy and phylogeny of Luxemburgiaceae (Ochnaceae). *Phytomorphology* 16: 39–55.
- Den Outer, R. W. & A. P. Vooren. 1980. Bark anatomy of some Sarcloaenaceae and Rhopalocarpaceae and their systematic position. *Meded. Landbouwhoogschool* 80(6): 3–15.
- DeVries, P. 1987. *The Butterflies of Costa Rica and Their Natural History*. Princeton Univ. Press, Princeton.
- Deyama, T., T. Ikawa & S. Nishibe. 1985. The constituents of *Eucommia ulmoides* Oliv. II. Isolation and structures of three new lignan glycosides. *Chem. Pharm. Bull.* 33: 3651–3657.
- Dickson, W. C. 1969. Comparative morphological studies in Dilleniaceae. VI. Stamens and young stem. *J. Arnold Arb.* 51: 403–418.
- . 1978. Comparative anatomy of Eucryphiaceae. *Amer. J. Bot.* 65: 722–735.
- . 1979. A survey of pollen morphology of the Conaraceae. *Pollen & Spores* 21: 31–79.
- . 1981. Contributions to the morphology and anatomy of *Strasburgeria* and a discussion of the taxonomic position of the Strasburgeriaceae. *Brittonia* 33: 564–580.
- . 1986. Further observations on the floral anatomy and pollen morphology of *Oncotheca* (Oncothecaceae). *Brittonia* 38: 249–259.
- . 1990. The morphology and relationships of *Medusagyne* (Medusagynaceae). *Pl. Syst. Evol.* 171: 27–55.
- & P. Baas. 1977. The morphology and relationships of *Paracryphia* (Paracryphiaceae). *Blumea* 23: 417–438.
- , J. W. Nowicke & J. J. Skvarla. 1982. Pollen morphology of the Dilleniaceae and Actiniaceae. *Amer. J. Bot.* 69: 1055–1073.
- Dileher, D. L. 1989. The occurrence of fruits with affinities to Ceratophyllaceae in Lower and Mid-Cretaceous sediments. *Amer. J. Bot.* 76 (Suppl., 6): 162. [Abstract.]
- & P. R. Crane. 1984. *Archaeanthus*: An early angiosperm from the Cenomanian of the Western Interior of North America. *Ann. Missouri Bot. Gard.* 71: 351–383.
- Ditsch, F. & W. Barthlott. 1994. *Mikromorphologie der*

- Epikuticularwachse und die Systematik der Dilleniales, Lecythidales, Malvales und Theales. *Trop. Subtrop. Pflanzenwelt* 88: 1-74.
- Domínguez, X. A., B. G. Espinoza, C. Rombold, W. Utz & H. Achenbach. 1992. Neolignans, norneolignans, and other compounds from *Krameria sonora*. *J. Med. Pl. Res.* 58: 332-333.
- Donoghue, M. J. & J. A. Doyle. 1989. Phylogenetic analysis of angiosperms and the relationships of Hamamelidaceae. Pp. 17-46 in P. R. Crane & S. Blackmore (editors), *Evolution, Systematics, and Fossil History of the Hamamelidaceae*, Vol. 1. Clarendon Press, Oxford.
- Downie, S. R. & J. D. Palmer. 1994. A chloroplast DNA phylogeny of the Caryophyllales based on structural and inverted repeat restriction site variation. *Syst. Bot.* 19: 236-252.
- Doyle, J. A. 1994. Origin of the angiosperm flower: A phylogenetic perspective. *Pl. Syst. Evol., Suppl.* 8: 7-29.
- . 1996. Seed plant phylogeny and the relationships of Gnetales. *Int. J. Pl. Sci.* 157 (Suppl., 6): S3-S39.
- & L. J. Hickey. 1975. Pollen and leaves from the Mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. Pp. 139-206 in C. B. Beck (editor), *Origin and Early Evolution of the Angiosperms*. Columbia Univ. Press, New York.
- , C. L. Hottel & J. V. Ward. 1990. Early Cretaceous tetrads, zonate pollen, and Winteraceae. II. Cladistic analysis and implications. *Amer. J. Bot.* 77: 1558-1568.
- , J. M. Donoghue & E. A. Zimmer. 1994. Integration of morphological and ribosomal RNA data on the origin of angiosperms. *Ann. Missouri Bot. Gard.* 81: 419-450.
- Drinan, A. N., P. R. Crane & S. B. Hoot. 1994. Patterns of floral evolution in the early diversification of non-magnoliid dicotyledons (eudicots). *Pl. Syst. Evol., Suppl.* 8: 93-122.
- , E. M. Friis & K. R. Pedersen. 1991. Angiosperm flowers and tricolpate pollen of buxaceous affinity from the Potomac Group (Mid-Cretaceous) of Eastern North America. *Amer. J. Bot.* 78: 153-176.
- Drude, O. 1891a. Clethraceae. Pp. 1-2 in A. Engler & K. Prantl (editors), *Die natürlichen Pflanzenfamilien*, 1st ed., Vol. IV/1. Engelmann, Leipzig.
- . 1891b. Ericaceae. Pp. 15-65 in A. Engler & K. Prantl (editors), *Die natürlichen Pflanzenfamilien*, 1st ed., Vol. IV/1. Engelmann, Leipzig.
- . 1891c. Epacridaceae. Pp. 66-84 in A. Engler & K. Prantl (editors), *Die natürlichen Pflanzenfamilien*, 1st ed., Vol. IV/1. Engelmann, Leipzig.
- Durand, R. & M. H. Zenk. 1974. The homogenisate ring-cleavage pathway in the biosynthesis of acetate-derived naphthoquinones of the Droseraceae. *Phytochemistry* 13: 1483-1492.
- Duvall, M. R., G. H. Learn, L. E. Eguiarte & M. T. Clegg. 1993a. Phylogenetic analysis of *rbcL* sequences identifies *Acorus calamus* as the primal extant monocotyledon. *Proc. Natl. Acad. Sci. U.S.A.* 90: 4641-4644.
- , M. T. Clegg, M. W. Chase, W. D. Clark, B. J. Kress, H. G. Hills, L. E. Eguiarte, J. F. Smith, B. S. Gaut, E. A. Zimmer & G. H. Learn, Jr. 1993b. Phylogenetic hypotheses for the monocotyledons constructed from *rbcL* sequence data. *Ann. Missouri Bot. Gard.* 80: 607-619.
- Ehrendorfer, F., W. Morawetz & J. Dawe. 1984. The neotropical angiosperm families Brunelliaceae and Caryocaraceae: First caryosystematical data and affinities. *Pl. Syst. Evol.* 145: 183-192.
- Eklund, H., E. M. Friis & K. R. Pedersen. 1997. Chloranthaceous floral structures from the Late Cretaceous of Sweden. *Pl. Syst. Evol.* 207: 13-42.
- Endress, P. K. 1980. The reproductive structures and systematic position of the Austrobaileyaceae. *Bot. Jahrb. Syst.* 101: 393-433.
- . 1986. Floral structure, systematics, and phylogeny in Trochodendrales. *Ann. Missouri Bot. Gard.* 73: 297-324.
- . 1987. The Chloranthaceae: Reproductive structures and phylogenetic position. *Bot. Jahrb. Syst.* 109: 153-226.
- . 1989. Aspects of evolutionary differentiation of the Hamamelidaceae and the Lower Hamamelididae. *Pl. Syst. Evol.* 162: 193-211.
- . 1993a. Austrobaileyaceae. Pp. 138-140 in K. Kubitzki (editor), *The Families and Genera of Vascular Plants*, Vol. 2. Springer, Berlin.
- . 1993b. Cercidiphyllaceae. Pp. 250-252 in K. Kubitzki (editor), *The Families and Genera of Vascular Plants*, Vol. 2. Springer, Berlin.
- . 1993c. Eupomatiaceae. Pp. 296-298 in K. Kubitzki (editor), *The Families and Genera of Vascular Plants*, Vol. 2. Springer, Berlin.
- . 1994a. Diversity and Evolutionary Biology of Tropical Flowers. Cambridge Univ. Press, Cambridge.
- . 1994b. Evolutionary aspects of the floral structure in *Ceratophyllum*. *Pl. Syst. Evol., Suppl.* 8: 175-183.
- . 1994c. Floral structure and evolution of primitive angiosperms: Recent advances. *Pl. Syst. Evol.* 192: 79-97.
- . 1994d. Shapes, sizes and evolutionary trends in stamens of Magnoliidae. *Bot. Jahrb. Syst.* 115: 429-460.
- & A. Igersheim. 1997. Gynoecium diversity and systematics of the Laurales. *Bot. J. Linn. Soc.* 125: 93-168.
- & S. Stumpf. 1991. The diversity of stamen structures in "Lower" Rosidae (Rosales, Fabales, Proteales, Sapindales). *Bot. J. Linn. Soc.* 107: 217-293.
- Engler, A. 1891. Saxifragaceae. Pp. 41-93 in A. Engler & K. Prantl (editors), *Die natürlichen Pflanzenfamilien*, 2nd ed. III., Vol. 2a. Engelmann, Leipzig.
- . 1925. Quinaeaceae. Pp. 106-108 in A. Engler & K. Prantl (editors), *Die natürlichen Pflanzenfamilien*, 2nd ed., Vol. 21. Engelmann, Leipzig.
- . 1930. Cunoniaceae. Pp. 229-262 in A. Engler & K. Prantl (editors), *Die natürlichen Pflanzenfamilien*, 2nd ed., Vol. 18a. Engelmann, Leipzig.
- & H. Melchior. 1925. Medusagynaceae. Pp. 50-52 in A. Engler & K. Prantl (editors), *Die natürlichen Pflanzenfamilien*, 2nd ed., Vol. 21. Engelmann, Leipzig.
- & K. Prantl (editors). 1887-1914. *Die natürlichen Pflanzenfamilien*, 1st ed. Engelmann, Leipzig.
- & ——— (editors). 1924-1995. *Die natürlichen Pflanzenfamilien*, 2nd ed. Engelmann, Leipzig.
- Erbar, C. & P. Leins. 1996. Distribution of the character states "early sympetal" and "late sympetal" within the "Sympetalae tetracycliae" and presumably allied groups. *Bot. Acta* 109: 427-440.
- Erdtman, G. 1952. *Pollen Morphology and Plant Taxonomy. An Introduction to Palynology*, I. Angiosperms. Almqvist & Wiksell, Stockholm.

- . 1958. A note on the pollen morphology in the Anastrocladaceae and Dioncophyllaceae. Veröff. Geobot. Inst. Rubel Zürich 33: 47–49.
- Fairbrothers, D. E. 1966. Serological correspondence of the genus *Corkia* with taxa of the Cornaceae, Nyssaceae and Garryaceae. Amer. J. Bot. 53: 637–638.
- Farr, D. F., G. F. Bills, G. P. Chamuris & A. Y. Rossman. 1989. Fungi on Plants and Plant Products in the United States. American Phytopathological Society Press, St. Paul.
- Farris, J. S. 1969. A successive approximations approach to character weighting. Syst. Zool. 18: 374–385.
- , V. A. Albert, M. Källersjö, D. Lipscomb & A. G. Kluge. 1997. Parsimony jackknifing outperforms neighbour-joining. Cladistics 12: 99–124.
- Fay, M. F., S. M. Swensen & M. W. Chase. 1997. Taxonomic affinities of *Medusagynne oppositifolia* (Medusagynaceae). Kew Bull. 52: 11–120.
- Fehrenbach, S. & W. Barthlott. 1988. Mikromorphologie der Epicuticular-Wachse der *Rosa* s. l. und deren systematische Gliederung. Bot. Jahrb. Syst. 109: 407–428.
- Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39: 783–791.
- Fernando, E. S., P. A. Gadek & C. J. Quinn. 1995. Simaroubaceae, an artificial construct: Evidence from *rbcl* sequence variation. Amer. J. Bot. 82: 92–103.
- Fieser, L. F. & E. M. Chamberlain. 1948. Synthesis of embelin, rapanone and related quinones by peroxide alkylation. J. Amer. Chem. Soc. 70: 71–75.
- Filho, W. W., A. I. Da Rocha, M. Yoshida & O. R. Gottlieb. 1985. Ellagic acid derivatives from *Rhabdophyllum macropphyllum*. Phytochemistry 24: 1991–1997.
- Fitch, W. M. 1971. Toward defining the course of evolution: Minimal change for a specific tree topology. Syst. Zool. 20: 406–416.
- Foster, A. S. & H. J. Arnott. 1960. Morphology and dichotomous vasculature of the leaf of *Kingdonia uniflora*. Amer. J. Bot. 47: 684–698.
- Franceschi, V. R. & H. T. Horner, Jr. 1980. Calcium oxalate crystals in plants. Bot. Rev. (Lancaster) 46: 361–428.
- Frehner, M., M. Scalet & E. E. Conn. 1990. Pattern of the cyanide-potential in developing fruits. Implications for plants accumulating cyanogenic monoglucosides (*Phaseolus lunatus*) or cyanogenic diglucosides in their seeds (*Linum usitatissimum*, *Prunus amygdalus*). Pl. Physiol. (Lancaster) 94: 28–34.
- Friis, E. M. 1984. Preliminary report of Upper Cretaceous angiosperm reproductive organs from Sweden and their level of organization. Ann. Missouri Bot. Gard. 71: 403–418.
- & P. K. Endress. 1990. Origin and evolution of angiosperm flowers. Advances Bot. Res. 17: 99–162.
- , K. R. Pedersen & P. R. Crane. 1994. Angiosperm floral structures from the Early Cretaceous of Portugal. Pl. Syst. Evol., Suppl. 8: 31–49.
- Gadek, P. A., C. J. Quinn, J. E. Rodman, K. G. Karol, E. Conti, R. A. Price & E. S. Fernando. 1992. Affinities of the Australian endemic Akaniaceae: New evidence from *rbcl* sequences. Austral. Syst. Bot. 5: 717–724.
- , E. S. Fernando, C. J. Quinn, S. B. Hoot, T. Terrazas, M. C. Sheahan & M. W. Chase. 1996. Sapindales: Molecular delimitation and infraordinal groups. Amer. J. Bot. 83: 802–811.
- Gagnepain, F., H. Humbert & H. Leconte (editors). 1907–1942. Flore générale de l'Indo-Chine. 8 Vols. Masson, Paris.
- Garratt, G. A. 1933. Systematic anatomy of the woods of the Myristicaceae. Trop. Woods 35: 6–47.
- Gavrilova, O. A. 1993. Types of pollen grain sculpture and their significance for systematics of the family Flacourtiaceae. Bot. Zhurn. (Moscow & Leningrad) 12: 45–52. [In Russian.]
- Geetha, K., I. Umadevi & M. Daniel. 1993. Primulales—A reassessment of the taxonomy and phylogeny of the group. Feddes Reper. 104: 67–71.
- Giannasi, D. E., G. Zurawski, G. Learn & M. T. Clegg. 1992. Evolutionary relationships of the Caryophyllidae based on comparative *rbcl* sequences. Syst. Bot. 17: 1–15.
- Gibbs, R. D. 1974. Chemotaxonomy of Flowering Plants, Vols. 1–4. McGill-Queens, Montreal.
- Gildemeister, E. & F. Hoffmann. 1956. Die ätherischen Öle, 4th ed. Akademie Verlag, Berlin.
- Gilg, E. 1925. Ochnaceae. Pp. 53–87 in A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed., Vol. 21. Engelmann, Leipzig.
- Goldblatt, P. & L. J. Dorr. 1986. Chromosome number in Sarcolaenaceae. Ann. Missouri Bot. Gard. 73: 828–829.
- & D. E. Johnson (editors). 1981/1984/1985/1988/1990/1991/1994. Index to Plant Chromosome Numbers. Monogr. Syst. Bot. Missouri Bot. Gard. 5: 1–533, 8: 1–427, 13: 1–224, 23: 1–264, 30: 1–243, 40: 1–238, 51: 1–267.
- Gore, U. R. 1935. Morphogenetic studies on the inflorescence of cotton. Bot. Gaz. 97: 118–138.
- Gottlieb, O. R., M. A. C. Kaplan, K. Kubitzki & J. R. Toledo Barros. 1988. Chemical dichotomies in the magnoliaceal complex. Nordie J. Bot. 8: 437–444.
- Gottwald, H. & N. Parameswaran. 1966. Das sekundäre Xylem der Familie Dipteroearpaeae. Anatomische Untersuchungen zur Taxonomie und Phylogenie. Bot. Jahrb. Syst. 85: 410–508.
- & ———. 1967. Beiträge zur Anatomie und Systematik der Quiinaeeae. Bot. Jahrb. Syst. 87: 361–381.
- & ———. 1968. Das sekundäre Xylem und die systematische Stellung der Anastrocladaceae und Dioncophyllaceae. Bot. Jahrb. Syst. 88: 42–69.
- Graur, D., L. Duret & M. Guoy. 1996. Phylogenetic position of the order Lagomorpha (rabbit, hares, and allies). Nature 379: 333–335.
- Grund, C. & U. Jensen. 1981. Systematic relationships of the Saxifragales revealed by serological characteristics of seed proteins. Pl. Syst. Evol. 137: 1–22.
- Gustafsson, M. H. G. & K. Bremer. 1995. Morphology and phylogenetic interrelationships of the Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, and related families (Asterales). Amer. J. Bot. 82: 250–265.
- Gutzwiller, M. A. 1961. Die phylogenetische Stellung von *Suriana maritima* L. Bot. Jahrb. Syst. 81: 1–49.
- Haber, J. M. 1959. The comparative anatomy and morphology of the flowers and inflorescences of the Proteaceae. I. Some Australian taxa. Phytomorphology 9: 325–358.
- . 1961. The comparative anatomy and morphology of the flowers and inflorescences of the Proteaceae. II. Some American taxa. Phytomorphology 11: 1–16, 16: 490–527.
- . 1966. The comparative anatomy and morphology of the flowers and inflorescences of the Proteaceae. III. Some African taxa. Phytomorphology 16: 490–527.

- Hagemann, W. 1970. Studien zur Entwicklungsgeschichte der Angiospermenblätter. Ein Beitrag zur Klärung ihres Gestaltungsprinzips. Bot. Jahrb. Syst. 90: 297-413.
- & S. Gleissberg. 1996. Organogenetic capacity of leaves: The significance of marginal blastozones in angiosperms. Pl. Syst. Evol. 199: 121-152.
- Hallier, H. 1914. Der Stammbaum des Pflanzenreichs. 14pp. in L. Reinhardt (editor), Vom Nebelfleck zum Menschen, 2nd ed., Vols. 2 and 3. Verlagsbuchhandlung Reinhardt, München.
- Harborne, J. B. 1969. Occurrence of flavonol 5-methyl ethers in higher plants and their systematic significance. Phytochemistry 8: 419-423.
- & H. Baxter. 1993. Phytochemical Dictionary. A Handbook to Bioactive Compounds from Plants. Taylor & Francis, London.
- Hayashi, H., M. Shiohira, T. Sakao, Y. Yamamura & H. Komae. 1980. An approach to chemotaxonomy of the *Asarum* subgenus *Heterotropa*. Biochem. Syst. & Ecol. 8: 109-113.
- Heel, W. A. van. 1966. Morphology of the androecium in Malvales. Blumea 13: 177-394.
- . 1967. Anatomical and ontogenetic investigations on the morphology of the flowers and the fruit of *Scyphostegia borneensis* Stapf (Scyphostegiaceae). Blumea 15: 107-125.
- . 1984. Flowers and fruits in Flacourtiaceae. V. The seed anatomy and pollen morphology of *Berberidopsis* and *Streptothamnus*. Blumea 30: 31-37.
- Hegnauer, R. 1962-1994. Chemotaxonomie der Pflanzen. 1-11a. Birkhäuser, Basel.
- Heimsch, C., Jr. 1942. Comparative anatomy of the secondary xylem in the Grinales and Terebinthales of Wettstein with reference to taxonomic grouping. Lilloa 8: 83-198.
- Heinig, K. H. 1951. Studies in the floral morphology of the Thymelaeaceae. Amer. J. Bot. 38: 113-132.
- Hekking, W. H. A. 1988. Violaceae. Part 1—*Rinorea* and *Rinoreocarpus*. Fl. Neotrop. Monogr. 46: 1-207.
- Hennig, S., W. Barthlott, I. Meusel & I. Theisen. 1994. Mikromorphologie der Epicuticularwachse und die Systematik der Magnoliidae, Ranunculidae und Hamamelidae. Trop. Subtrop. Pflanzenwelt 90: 1-60.
- Heo, K. & H. Tobe. 1994. Embryology and relationships of *Suriana maritima* L. (Surianaceae). J. Pl. Res. 107: 29-37.
- Heywood, V. H. (editor). 1978. Flowering Plants of the World. Oxford Univ. Press, Oxford.
- Hickey, L. J. & J. A. Wolfe. 1975. The bases of angiosperm phylogeny: Vegetative morphology. Ann. Missouri Bot. Gard. 62: 538-589.
- Hideux, M. J. & I. K. Ferguson. 1976. The stereostructure of the exine and its evolutionary significance in Saxifragaceae s.l. Pp. 327-378 in I. K. Ferguson & J. Muller (editors), The Evolutionary Significance of the Exine. Academic Press, New York.
- Hill, A. E. & B. S. Hill. 1976. Mineral Ions. Pp. 225-243 in U. Lüttge & M. G. Pitman (editors), Encyclopedia of Plant Physiology. New Series. Vol. 2: Transport in Plants II, Part B, Tissues and Organs. Springer, Berlin.
- Hillebrand, G. R. & D. E. Fairbrothers. 1966. Phytosociological systematic studies of selected genera of the Rubiales and Umbellales. Amer. J. Bot. 53: 638.
- & ———. 1970. Serological investigation on the systematic position of the Caprifoliaceae. I. Correspondence with selected Rubiaceae and Cornaceae. Amer. J. Bot. 57: 810-815.
- Hillis, D. M. 1996. Inferring complex phylogenies. Nature 383: 130-131.
- Hirmer, M. 1918. Beiträge zur Morphologie der polyandrischen Blüten. Flora 110: 140-192.
- Huang, T.-C. 1972. Pollen Flora of Taiwan. National Taiwan Univ., Botany Department Press.
- Huber, H. 1991. Angiospermen. Leitfaden durch die Ordnungen und Familien der Bedecktsamer. Fischer, Stuttgart.
- . 1993. Aristolochiaceae. Pp. 129-137 in K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.
- Hufford, L. D. 1992. Rosidae and their relationships to other nonmagnoliid dicotyledons: A phylogenetic analysis using morphological and chemical data. Ann. Missouri Bot. Gard. 79: 218-248.
- . 1996. The morphology and evolution of male reproductive structures of Gnetales. Int. J. Pl. Sci. 157: S95-S112.
- & P. K. Endress. 1989. The diversity of anther structures and dehiscence patterns among Hamamelidaceae. Bot. J. Linn. Soc. 99: 301-346.
- Humphrey, R. R. 1935. A study of *Idria columnaris* and *Fouquieria splendens*. Amer. J. Bot. 22: 184-207.
- Hutchinson, J. 1964/1967. The Genera of Flowering Plants. Dicotyledons. Vols. 1 and 2. Clarendon Press, Oxford.
- . 1973. The Families of Flowering Plants Arranged According to a New System Based on Their Probable Phylogeny, 3rd ed. Clarendon Press, Oxford.
- Huynh, K.-L. 1969. Etude du pollen des Oxalidaceae. Bot. Jahrb. Syst. 89: 272-303.
- Ilic, J. 1991. CSIRO Atlas of Hardwoods. Springer, Berlin.
- Ionescu, F., S. D. Jolad & J. R. Cole. 1977. Dehydrodiisoeugenol: A naturally occurring lignan from *Aristolochia talisana* (Aristolochiaceae). J. Pharm. Sci. 66: 1489-1490.
- Jäger-Zürn, I. 1966. Infloreszenz- und blütenmorphologische, sowie embryologische Untersuchungen an *Myrothamnus* Welw. Beitr. Biol. Pflanzen 42: 241-271.
- Janchen, E. 1909. Die Cistaceen Oesterreich-Ungarns. Mitt. Naturwiss. Vereins Univ. Wien 7: 1-124.
- . 1925. Cistaceae. Pp. 289-313 in A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed., Vol. 21. Engelmann, Leipzig.
- Jensen, S. R., S. E. Lyse-Pedersen & B. J. Nielsen. 1979. Novel bis-irradioid glucosides from *Dipsacus sylvestris*. Phytochemistry 18: 273-277.
- Jensen, U. & B. Greven. 1984. Serological aspects and phylogenetic relationships of the Magnoliidae. Taxon 33: 563-577.
- John, J. & K. P. Kolbe. 1980. The systematic position of the "Theales" from the viewpoint of serology. Biochem. Syst. & Ecol. 8: 241-248.
- Johri, B. M. 1970. Symposium on comparative embryology of angiosperms. Proc. Indian Natl. Sci. Acad., B 41: 1-385.
- & D. Kak. 1954. The embryology of *Tamarix* L. Phytomorphology 4: 230-247.
- , K. B. Ambegoakar & P. S. Srivastava. 1992. Comparative Embryology of Angiosperms, Vols. 1 and 2. Springer, Berlin.
- , R. N. Kapil, S. P. Bhatnagar, N. N. Bhandari & M. R. Vijayaraghavan (editors). 1967. Seminar on

- Comparative Embryology of Angiosperms. Department of Botany, Univ. Press, Delhi.
- Juniper, B. E., R. J. Robins & D. M. Joel. 1989. The Carnivorous Plants. Academic Press, London.
- Kamelina, O. P., V. A. Poddubnaya-Arnoldi, A. L. Takhtajian, M. S. Yakovlev & G. Y. Zhukova. 1983. Comparative Embryology of the Flowering Plants. Phytolaccaeae-Thymelaeaeae. Nauka, Leningrad. [In Russian.]
- , I. D. Romanov, A. L. Takhtajan, M. S. Yakovlev & G. Y. Zhukova. 1981. Comparative Embryology of the Flowering Plants. Winteraceae-Juglandaceae. Nauka, Leningrad. [In Russian.]
- Kanis, A. 1968. A revision of the Ochnaceae of the Indo-Pacific Area. *Blumea* 16: 1-82.
- Kapil, R. N. & A. K. Bhatnagar. 1991. Embryological evidence in angiosperm classification and phylogeny. *Bot. Jahrb. Syst.* 113: 309-338.
- & R. Maheshwari. 1965. Embryology of *Helianthemum vulgare* Gaertn. *Phytomorphology* 14: 547-557.
- Kaur, H. 1969. Embryological investigations on *Bixa orellana* L. *Proc. Natl. Inst. Sci. India* 35: 487-506.
- Keating, R. C. 1972. The comparative morphology of the Cochlospermaceae. III. The flower and pollen. *Ann. Missouri Bot. Gard.* 59: 282-296.
- . 1975. Trends of specialization in pollen of Flacourtiaceae with comparative observations of Cochlospermaceae and Bixaceae. *Grana* 15: 29-49.
- Keefe, J. M. & M. F. Moseley. 1978. Wood anatomy and phylogeny of *Paeonia* section *Moutan*. *J. Arnold Arb.* 59: 274-297.
- Keller, K. 1982. Untersuchungen zum  $\beta$ -Asarongehalt handelsüblicher Kalmusdrogen sowie zu den Inhaltsstoffen des asaronfreien Kalmus. Unpublished Ph.D. Thesis, University of Saarbrücken.
- Keng, H. 1962. Comparative morphological studies in Theaceae. *Univ. Calif. Publ. Bot.* 33: 269-383.
- Kessler, P. J. A. 1993. Menispermaceae. Pp. 93-128 in K. Kubitzki (editor), *The Families and Genera of Vascular Plants*, Vol. 2. Springer, Berlin.
- Klucking, E. P. 1986/1987/1988/1989/1991/1992/1995. Leaf Venation Patterns. 1. Annonaceae/ 2. Lauraceae/ 3. Myrtaceae/ 4. Melastomataceae/ 5. Combretaceae/ 6. Flacourtiaceae/ 7. The Classification of Leaf Venation Patterns. Cramer, Stuttgart.
- Kobuski, C. E. 1951. Studies in the Theaceae, XXIII. The genus *Pelliciera*. *J. Arnold Arb.* 32: 256-262.
- Köhler, E. 1994. Parallel evolution of pollen characters in the genus *Buxus* L. (Buxaceae). *Acta Bot. Gallica* 141: 223-232.
- Kolbe, K. P. & J. John. 1979a. Serologische Untersuchungen zur Systematik der Violales. *Bot. Jahrb. Syst.* 101: 3-15.
- & ———. 1979b. Serology and systematics of the Ebenales and Theales. *Biochem. Syst. & Ecol.* 8: 249-256.
- Kostermans, A. J. G. H. 1985. Family status for the Monotoideae Gilg and the Pakaraimoideae Ashton, Maguire and de Zeeuw (Dipterocarpaceae). *Taxon* 34: 426-435.
- Kribs, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. *Bot. Gaz.* 96: 547-557.
- Kron, K. A. & M. W. Chase. 1993. Systematics of the Ericaceae, Empetraceae, Epacridaceae and related taxa based upon *rbcL* sequence data. *Ann. Missouri Bot. Gard.* 80: 735-741.
- Kubitzki, K. 1993a. Calycanthaceae. Pp. 197-200 in K. Kubitzki (editor), *The Families and Genera of Vascular Plants*, Vol. 2. Springer, Berlin.
- . 1993b. Canellaceae. Pp. 200-203 in K. Kubitzki (editor), *The Families and Genera of Vascular Plants*, Vol. 2. Springer, Berlin.
- . 1993c. Degeneriaceae. Pp. 290-291 in K. Kubitzki (editor), *The Families and Genera of Vascular Plants*, Vol. 2. Springer, Berlin.
- , P. von Sengbush & H.-H. Poppendieck. 1991. Parallelism, its evolutionary origin and systematic significance. *Aliso* 13: 191-206.
- Kuprianova, L. A. 1979. On the possibility of the development of tricolpate pollen from monosulcate. *Grana* 18: 1-4.
- Landsmann, J., E. S. Dennis, T. J. V. Higgins, C. A. Appleby, A. A. Korrt & W. J. Peacock. 1986. Common evolutionary origin of legume and non-legume plant haemoglobins. *Nature* 324: 166-168.
- Lavault, M. & J. Bruneton. 1980. Isolement de deux nouveaux alcaloïdes, triphypelline et O-méthyl-5'-triphypelline. *J. Med. Pl. Res.* 38, Suppl.: 17-21.
- Le Quesne, P. W., J. E. Larrahondo & R. F. Raffauf. 1980. Antitumor plants. X. Constituents of *Nectandra rigida*. *J. Nat. Prod. (Lloydia)* 43: 353-359.
- Lebreton, P. & M. P. Bouchez. 1967. Recherches chimiotaxonomiques sur les plantes vasculaires 5. Distribution des composés polyphénoliques chez les Parietales. *Phytochemistry* 6: 1601-1608.
- Leenhouts, P. W. 1956. Some notes on the genus *Dichapetalum* (Dichapetalaceae) in Asia, Australia, and Melanesia. *Reinwardtia* 4: 75-87.
- Lenke, D. E. 1988. A synopsis of Flacourtiaceae. *Aliso* 12: 29-43.
- Les, D. H. 1988. The origin and affinities of the Ceratophyllaceae. *Taxon* 37: 326-345.
- . 1993. Ceratophyllaceae. Pp. 246-250 in K. Kubitzki (editor), *The Families and Genera of Vascular Plants*, Vol. 2. Springer, Berlin.
- & C. T. Philbrick. 1996. The phylogeny of riverweeds (Podostemaceae): Insights from *rbcL* sequence data. *Amer. J. Bot.* 83: 174. [Abstract.]
- , D. K. Garvin & C. F. Wimpee. 1991. Molecular evolutionary history of ancient aquatic angiosperms. *Proc. Natl. Acad. Sci. U.S.A.* 88: 10119-10123.
- Letouzey, R. 1961. Notes sur les Scytopetalacées (Révision des Scytopetalacées de l'herbier de Paris). *Adansonia n. s.* 1: 106-142.
- Levin, G. A. 1986. Systematic foliar morphology of Phyllanthoideae (Euphorbiaceae). I. Conspectus. *Ann. Missouri Bot. Gard.* 73: 29-85.
- Lin, C. M., Z. Q. Liu & S. D. King. 1986. *Nicotiana* chloroplast genome: X. Correlation between the DNA sequences and the isoelectric focusing pattern of the LS of rubisco. *Pl. Molec. Biol.* 6: 81-87.
- Maddison, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. *Syst. Zool.* 40: 315-328.
- Maddison, W. P. & D. R. Maddison. 1992. *MacClade*, Version 3. Analysis of Phylogeny and Character Evolution. Sinauer, Sunderland, Massachusetts.
- Maguire, B. & P. S. Ashton. 1980. *Pakaraimaea dipterocarpacea* II. *Taxon* 29: 225-231.
- et al. 1972. Botany of the Guyana Highland—Part IX. Tetrameristaceae. *Mem. New York Bot. Gard.* 23: 165-192.
- Martius, C. F. P. von (editor). 1840-1906. *Flora Bras-*

- iliensis: enumeratio plantarum in Brasilia, Vols. 1–15. Fleischer, München.
- Mauritzon, J. 1935. Zur Embryologie der Elaeocarpaceae. Ark. Bot. 26A (10): 1–8.
- . 1936. Zur Embryologie und systematischen Abgrenzung der Reihen Terebinthales und Celastrales. Bot. Not. 1936: 161–211.
- Maury, G., J. Muller & B. Lugardon. 1975. Notes on the morphology and fine structure of the exine of some pollen types in Dipterocarpaceae. Rev. Palaeobot. Palynol. 19: 241–289.
- Mc Nair, J. B. 1930. The taxonomic and climatic distribution of oil and starch in seeds in relation to the physical and chemical properties of both substances. Amer. J. Bot. 17: 662–668.
- McAlpine, J. B., N. V. Riggs & (in part) P. G. Gordon. 1968. Absolute stereochemistry of caloptin. Austral. J. Chem. 21: 2095–2106.
- Melchior, H. (editor). 1964. A. Engler's Syllabus der Pflanzenfamilien, H. Bornträger, Berlin.
- Menega, A. M. W. 1982. Stem structure of the New World Menispermaceae. J. Arnold Arb. 63: 145–171.
- Metcalfe, C. R. 1952. *Medusandra richardsiana* Brenan. Anatomy of the leaf, stem and wood. Kew Bull. 9: 237–246.
- . 1956. *Scyphostegia borneensis* Stapf. Anatomy of stem and leaf in relation to its taxonomic position. Reinwardtia 4: 99–104.
- . 1962. Notes on the systematic anatomy of *Whittonia* and *Peridiscus*. Kew Bull. 15: 472–475.
- . 1987. Anatomy of the Dicotyledons, 2nd ed., Vol. 3. Magnoliales, Illiciales, and Laurales. Clarendon Press, Oxford.
- & L. Chalk. 1950. Anatomy of the Dicotyledons. Leaves, Stem, and Wood in Relation to Taxonomy with Notes on Economic Uses, 1st ed., Vols. 1 and 2. Clarendon Press, Oxford.
- & L. Chalk. 1988/1989. Anatomy of the Dicotyledons, 2nd ed., Vols. 1 and 2. Oxford Univ. Press, Oxford.
- Meylan, B. A. & B. G. Butterfield. 1978. The structure of New Zealand woods. New Zealand Dept. Sci. Industr. Res. Inform. Ser. 222: 1–250.
- Miller, R. B. 1975. Systematic anatomy of the xylem and comments on the relationships of Flacourtiaceae. J. Arnold Arb. 56: 20–102.
- Mkpong, O. E., H. Yan, G. Chism & R. T. Sayre. 1990. Purification, characterization and localization of linamarase in Cassava. Pl. Physiol. (Lancaster). 93: 176–181.
- Morawetz, W. 1981. Zur systematischen Stellung der Gattung *Prockia*: Karyologie und Epidermisstruktur im Vergleich zu *Flacourtia* (Flacourtiaceae), *Grewia* (Tiliaceae) und verwandten Gattungen. Pl. Syst. Evol. 139: 57–76.
- Morgan, D. R. & D. E. Soltis. 1993. Phylogenetic relationships among members of Saxifragaceae sensu lato based on *rbcL* sequence data. Ann. Missouri Bot. Gard. 80: 631–660.
- & K. R. Robertson. 1994. Systematic and evolutionary implications of *rbcL* sequence variation in Rosaceae. Amer. J. Bot. 81: 890–903.
- Morton, C. M. 1995. A new genus and species of Dipterocarpaceae from the Neotropics. II. Stem anatomy. Brittonia 47: 237–247.
- , S. A. Mori, G. T. Prance, K. G. Karol & M. W. Chase. 1997. Phylogenetic relationships of Lecythida-  
ceae: A cladistic analysis using *rbcL* sequence and morphological data. Amer. J. Bot. 84: 530–540.
- Murai, F., M. Tagawa, S. Matsuda, T. Kikuchi, S. Uesato & H. Inouye. 1985. Abeliosides A and B, secoiridoid glucosides from *Abelia grandiflora*. Phytochemistry 24: 2329–2335.
- Nandi, O. I. 1998a. Ovule and seed anatomy of Cistaceae and related Malvaceae. Pl. Syst. Evol. (in press).
- . 1998b. Floral development and systematics of Cistaceae. Pl. Syst. Evol. (in press).
- Netolitzky, F. 1926. Anatomie der Angiospermen-Samen. Bornträger, Berlin.
- Nickrent, D. L. 1996. Phylogenetic relationships of parasitic Santalales and Rafflesiaceae inferred from 18S rRNA sequences. Amer. J. Bot. 83 (Suppl., 6): 212. [Abstract.]
- Nixon, K. C. & J. I. Davis. 1991. Polymorphic taxa, missing values, and cladistic analysis. Cladistics 7: 233–241.
- , W. L. Crepet, D. Stevenson & E. M. Friis. 1994. A reevaluation of seed plant phylogeny. Ann. Missouri Bot. Gard. 81: 484–533.
- Olmstead, R. G., B. Bremer, K. M. Scott & J. D. Palmer. 1993. A parsimony analysis of the Asteridae sensu lato based on *rbcL* sequences. Ann. Missouri Bot. Gard. 80: 700–722.
- , H. J. Michaels, K. M. Scott & J. D. Palmer. 1992. Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbcL*. Ann. Missouri Bot. Gard. 79: 249–265.
- Oxelman, B. & M. Lidén. 1995. The position of *Circaeaster*—Evidence from nuclear ribosomal DNA. Pl. Syst. Evol., Suppl. 9: 189–193.
- Payer, J.-B. 1857. Traité d'organogénie comparée de la fleur. Masson, Paris.
- Philipson, W. R. 1993. Amborellaceae, Pp. 92–93 in K. Kubitzki (editor), The Families and Genera of Vascular Plants, Vol. 2. Springer, Berlin.
- Piccioli, L. 1901. Il legno e la corteccia delle Cistaceae. Nuovo Giorn. Bot. Ital. n.s. 8: 473–504.
- Pierre, J. 1984. Systématique évolutive cladistique et mimétisme chez les lépidoptères du genre *Acræa*. Unpublished Ph.D. Thesis, University of Paris.
- Pilger, R. 1925a. Bixaceae, Pp. 313–315 in A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed., Vol. 21. Engelmann, Leipzig.
- . 1925b. Cochlospermaceae, Pp. 316–320 in A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, 2nd ed., Vol. 21. Engelmann, Leipzig.
- Prance, G. T. 1968. The systematic position of *Rhabdodendron* Gilg & Pilg. Bull. Jard. Bot. Belg. 38: 127–146.
- . 1972. Rhabdodendraceae. Fl. Neotrop. Monogr. 11: 1–21.
- & M. F. da Silva. 1973. Caryocaraceae. Fl. Neotrop. Monogr. 12: 1–75.
- Price, R. A. & J. D. Palmer. 1993. Phylogenetic relationships of the Geraniaceae and Geraniales from *rbcL* sequence comparisons. Ann. Missouri Bot. Gard. 80: 661–671.
- Proctor, M. C. F. 1955. Some chromosome counts in the European Cistaceae. Watsonia 3: 154–159.
- Puff, C. & A. Weber. 1976. Contributions to the morphology, anatomy, and karyology of *Rhabdodendron*, and a reconsideration of the systematic position of the Rhabdodendraceae. Pl. Syst. Evol. 125: 195–221.
- Qiu, Y.-L., M. W. Chase, D. H. Les & C. R. Parks. 1993.

- Molecular phylogenetics of the Magnoliidae: Cladistic analyses of nucleotide sequences of the plastid gene *rbcL*. *Ann. Missouri Bot. Gard.* 80: 587-606.
- Rao, K. V. & F. M. Alvarez. 1982. Chemistry of *Saururus cernuus*. I. Saucermetin, a new neolignan. *J. Nat. Prod. (Lloydia)* 45: 393-397.
- Rao, T. A. 1991. *Compendium of Foliar Sclereids in Angiosperms: Morphology and Taxonomy*. Wiley & Sons, New Delhi.
- Raynal-Roques, A. 1981. Contribution à l'Étude Biomorphologique des Angiospermes Aquatiques Tropicales—Essai d'Analyse de l'Évolution, Vol. I. Unpublished Ph.D. Thesis, University of Montpellier. Atelier Duplication, Montpellier.
- Record, S. J. 1933. The woods of *Rhabdodendron* and *Duckeodendron*. *Trop. Woods* 33: 6-10.
- Reidt, G. 1997. Fruchtanatomische Studien an den "klassisch" gefassten Cornaceae s.l. in E. Smets, L. P. Ronse Decraene & E. Robbrecht (editors), 13th Symposium of Morphology, Anatomy & Systematics, Program & Abstracts. *Scripta Bot. Belg.* 15: 134.
- Rendle, A. B., G. Baker & S. M. Moore. 1921. Systematic account of the plants collected in New Caledonia and the Islands of Pines by Prof. R. H. Compton, M. A., in 1914. *J. Linn. Soc., Bot.* 45: 246-417.
- Ricci, I. 1957. *Morphologia e costituzione chimica dei pelli nel genere Cistus e loro importanza nella sistematica di alcune specie*. *Ann. Bot. (Rome)* 25: 540-566.
- Rice, K. A., M. J. Donoghue & R. G. Olmstead. 1995. A reanalysis of the large *rbcL* dataset. *Amer. J. Bot.* 82 (Suppl., 6): 156-157. [Abstract.]
- Rodman, J., R. A. Price, K. Kenneth, E. Conti, K. J. Sysma & J. D. Palmer. 1993. Nucleotide sequences of the *rbcL* gene indicate monophyly of mustard oil plants. *Ann. Missouri Bot. Gard.* 80: 686-699.
- Rohwer, J. G. 1996. A preliminary survey of the fruits and seeds of the Oleaceae. *Bot. Jahrb. Syst.* 115: 271-291.
- Ronse Decraene, L. P. 1989. The floral development of *Cochlospermum tinctorium* and *Bixa orellana* with special emphasis on the androecium. *Amer. J. Bot.* 76: 1344-1359.
- . 1992. The Androecium of the Magnoliophytina: Characterization and Systematic Importance. Unpublished Ph.D. Thesis, University of Leuven, Belgium.
- & E. F. Smets. 1992. Complex polyandry in the Magnoliatae: Definition, distribution and systematic value. *Nordic J. Bot.* 12: 621-649.
- Rutishauser, R. 1997. Structure and developmental diversity in Podostemaceae (river-weeds). *Aquatic Bot.* 57: 29-70.
- & R. Sattler. 1987. Complementary and heuristic value of contrasting models in structural botany. II. Case study on leaf whorls: *Equisetum* and *Ceratophyllum*. *Bot. Jahrb. Syst.* 109: 227-256.
- Sáenz de Rivas, C. 1979. Pollen morphology of Spanish Cistaceae. *Grana* 18: 91-98.
- Sampson, E. B. 1993. Pollen morphology of the Amborellaceae and Hortoniaceae (Hortonioidae: Monimiaceae). *Grana* 32: 154-162.
- & P. K. Endress. 1984. Pollen morphology in the Trimeniaceae. *Grana* 23: 129-137.
- Sandwich, N. Y. 1962. Contribution to the flora of tropical America. LXIX. A new genus of Peridiscaceae. *Kew Bull.* 15: 467-471.
- Satabié, B. 1974. Contribution de la palynologie à l'étude des Irvingiacées d'Afrique tropicale. *Adansonia n.s.* 14: 277-289.
- Sattler, R. 1973. *Organogenesis of Flowers*, a Photographic Text-Atlas. Univ. Toronto Press, Toronto.
- Saunders, E. R. 1937. The vascular ground plan as a guide to the floral ground plan: Illustrated from Cistaceae. *New Phytol.* 35: 47-67.
- . 1937-1939. *Floral Morphology. A New Outlook with Special Reference to the Interpretation of the Gynaecium*. Vols. 1 and 2. Heffer, Cambridge.
- Savolainen, V., J. F. Amann, E. Douzery & R. Spichiger. 1994. Molecular phylogeny of families related to Celastrales based on *rbcL* 5' flanking sequences. *Molec. Phylog. & Evol.* 3: 27-37.
- , C. M. Morton, S. B. Hoot & M. W. Chase. 1996. An examination of phylogenetic patterns of plastid *atpB* gene sequences among eudicots. *Amer. J. Bot.* 83 (Suppl., 6): 190. [Abstract.]
- Schacppi, H. 1953. Morphologische Untersuchungen an den Karpellen der Calycanthaceae. *Phytomorphology* 3: 112-117.
- Schmid, R. 1964. Die systematische Stellung der Dioncophyllaceen. *Bot. Jahrb. Syst.* 83: 1-56.
- Schnarf, K. 1931. Vergleichende Embryologie der Angiospermen. *Borntraeger*, Berlin.
- Schweingruber, F. H. 1990. *Anatomy of European Woods*. Haupt, Bern.
- Selmar, D. 1993. Transport of cyanogenic glucosides: Linustatin uptake by *Hevea* cotyledons. *Planta* 191: 191-199.
- Sethi, M. L., G. S. Rao, B. K. Chowdhury, J. F. Morton & G. J. Kapadia. 1976. Identification of volatile constituents of *Sassafras albidum* root oil. *Phytochemistry* 15: 1773-1775.
- Setoguchi, H., H. Tobe & H. Ohba. 1992. Seed coat anatomy of *Crossostylis* Rhizophoraceae: Its evolutionary and systematic implications. *Bot. Mag. (Tokyo)* 105: 625-638.
- Seubert, E. 1993. *Die Samen der Araceen*. Koeltz, Königstein.
- Sévenet, T., C. Thal & P. Potier. 1971. Isolement et structure du cantleyoside, nouveau glucoside terpénique de *Cantleya corniculata* (Becc.) Howard (Icacinacées). *Tetrahedron* 27: 663-668.
- Shiklina, I. A. 1977. The comparative anatomy of the wood of the genus *Oncothea* (order Theales). *Bot. Zhurn. (Moscow & Leningrad)* 62: 1273-1275. [In Russian.]
- Simon, J. P. 1970. Comparative serology of the order Nymphaeales. I. Preliminary survey on the relationships of *Nelumbo*. *Aliso* 7: 243-261.
- . 1971. Comparative serology of the order Nymphaeales II: Relationships of Nymphaeaceae and Nelumbonaceae. *Aliso* 7: 325-350.
- Sinnott, E. W. 1914. Investigations on the phylogeny of the angiosperms. I. The anatomy of the node as an aid in the classification of angiosperms. *Amer. J. Bot.* 1: 303-322.
- Smith, C. R., Jr., D. Weisleder & R. W. Miller. 1980. Linustatin and neolinstatin: Cyanogenic glucosides of linessed meal that protect animals against selenium toxicity. *J. Organic Chem.* 45: 507-510.
- Solereder, H. 1899/1908. *Systematische Anatomie der Dicotyledonen*. Vols. 1 and 2. Enke, Stuttgart.
- & J. F. Meyer. 1928. *Systematische Anatomie der Monokotyledonen*. Heft III. *Principes—Synanthae—Späthlorae*. Bornträger, Berlin.

- Soltis, D. E. & P. S. Soltis. 1997. Phylogenetic relationships in Saxifragaceae sensu lato: A comparison of topologies based on 18S rDNA and *rbcl* sequences. *Amer. J. Bot.* 84: 504-523.
- , Q.-Y. Xiang & L. Hufford. 1995a. Relationships and evolution of Hydrangeaceae based on *rbcl* sequence data. *Amer. J. Bot.* 82: 504-514.
- , C. Hibsich-Jetter, P. S. Soltis, M. W. Chase & J. S. Farris. 1997a. Molecular phylogenetic relationships among angiosperms: An overview based on *rbcl* and 18S rDNA sequences. Pp. 157-178 in K. Iwatsuki & P. H. Raven (editors), *Evolution and Diversification of Land Plants*. Springer, Tokyo.
- , P. S. Soltis, D. R. Morgan, S. M. Swensen, B. C. Mullin, J. M. Dowd & P. G. Martin. 1995b. Chloroplast gene sequence data suggest a single origin of the pre-disposition for symbiotic nitrogen fixation in angiosperms. *Proc. Natl. Acad. Sci. U.S.A.* 92: 2647-2651.
- , P. S. Soltis, M. Mort, M. W. Chase, V. Savolainen, S. B. Hoot & C. M. Morton. Inferring complex phylogenies: An empirical approach using three large DNA sets for angiosperms. *Syst. Biol.* (in press).
- , P. S. Soltis, D. L. Nickrent, L. A. Johnson, W. J. Hahn, S. B. Hoot, J. A. Sweere, R. K. Kuzoff, K. A. Kron, M. W. Chase, S. M. Swensen, E. A. Zimmer, S.-M. Chaw, L. J. Gillespie, W. J. Kress & K. J. Sytsma. 1997b. Angiosperm phylogeny inferred from 18S ribosomal DNA sequences. *Ann. Missouri Bot. Gard.* 84: 1-49.
- Souèges, R. 1937. Développement de l'embryon chez *Helianthemum guttatum*. *Bull. Soc. Bot. France* 84: 400.
- Sprent, J. I. & D. McKey (editors). 1994. *Advances in Legume Systematics*, Part 5. The Nitrogen Factor. Royal Botanic Gardens, Kew.
- Stearn, F. C. 1946. A Study of the Genus *Paeonia*. The Royal Horticultural Society, London.
- Stevens, P. F. 1991. On the phylogeny of the Elatinaceae-Bonnetiaceae-Clusiaceae. *Amer. J. Bot.* 78 (Suppl., 6): 220. [Abstract.]
- Sutter, D. & P. K. Endress. 1995. Aspects of gynoecium structure and macrosystematics in Euphorbiaceae. *Bot. Jahrb. Syst.* 116: 517-536.
- Swensen, S. M., B. C. Mullin & M. W. Chase. 1994. Phylogenetic affinities of Datisceae based on an analysis of nucleotide sequences from the plastid *rbcl* gene. *Syst. Bot.* 19: 157-168.
- Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.
- Sytsma, K. J. & D. A. Baum. 1996. Molecular phylogenies and the diversification of the angiosperms. Pp. 314-340 in D. W. Taylor & L. J. Hickey (editors), *Flowering Plant Origin, Evolution and Phylogeny*. Chapman & Hall, New York.
- Syvanen, M. 1994. Horizontal gene transfer: Evidence and possible consequences. *Annual Rev. Genet.* 28: 237-261.
- , H. Hartmen & P. F. Stevens. 1989. Classical plant taxonomic ambiguities extend to the molecular level. *J. Molec. Evol.* 28: 536-544.
- Takahashi, A. 1985. Wood anatomical studies of Polycarpiceae. I. Magnoliales. *Sci. Rep. Osaka Univ.* 34: 29-83.
- Takahashi, K. & K. Sohma. 1982. Pollen morphology of the Droseraceae and its related taxa. *Sci. Rep. Tohoku Imp. Univ., Ser. 4, Biology* 38: 81-156.
- Takhtajan, A. L. 1966. *Systema et phylogenia Magnoliophytorum*. Nauka, Moscow. [In Russian.]
- . 1987. *The System of the Magnoliophytes*. Nauka, Leningrad. [In Russian.]
- (editor). 1985/1988/1991. *Comparative Anatomy of Seeds*, Vols. 1-3. Nauka, Leningrad. [In Russian.]
- . 1997. *Diversity and Classification of Flowering Plants*. Columbia Univ. Press, New York.
- , N. R. Meyer & V. N. Kosenko. 1985. The pollen morphology and classification in Rafflesiaceae s.l. *Bot. Zhurn. (Moscow & Leningrad)* 70: 153-168. [In Russian.]
- Tang, Y. 1994. Embryology of *Plagiopteris suaveolens* Griffith (Plagiopteridaceae) and its systematic implications. *Bot. J. Linn. Soc.* 116: 145-157.
- Taylor, D. W. & L. J. Hickey. 1996. Evidence for and implications of an herbaceous origin for angiosperms. Pp. 116-140 in D. W. Taylor & L. J. Hickey (editors), *Flowering Plant Origin, Evolution & Phylogeny*. Chapman & Hall, New York.
- Taylor, F. H. 1972. The secondary xylem of the Violaceae: A comparative study. *Bot. Gaz.* 133: 230-242.
- Thanikaioni, G. 1986. Evolution of Menispermaceae. *Canad. J. Bot.* 64: 3130-3133.
- Theisen, I. & W. Barthlott. 1994. Mikromorphologie der Epicutikularwache und die Systematik der Gentianales, Rubiales, Dipsacales und Calycerales. *Trop. Subtrop. Pflanzenwelt* 39: 1-62.
- Thieme, H. & R. Benecke. 1966. Isolierung eines neuen Phenolglykosides aus *Populus nigra* L. *Pharmazie* 21: 59-60.
- & ———. 1970. Ueber die Identität der Glucoside Xylosmosid und Poliothysid mit Nigracin. *Pharmazie* 25: 492.
- Thorne, R. F. 1983. Proposed new realignments in the angiosperms. *Nordic J. Bot.* 3: 85-117.
- . 1992. Classification and geography of the flowering plants. *Bot. Rev. (Lancaster)* 58: 225-348.
- Tobe, H. & C.-I. Peng. 1990. The embryology and taxonomic relationships of *Bretschneidera* (Bretschneideraceae). *Bot. J. Linn. Soc.* 193: 139-152.
- & P. H. Raven. 1995. Embryology and relationships of *Akania* (Akanaceae). *Bot. J. Linn. Soc.* 118: 261-274.
- Todzia, C. A. 1993. Chloranthaceae. Pp. 281-287 in K. Kubitzki (editor), *The Families and Genera of Vascular Plants*, Vol. 2. Springer, Berlin.
- Tomlinson, P. B. 1961. *Anatomy of the Monocotyledons. II Palmae*. Oxford Univ. Press, London.
- Tsou, C.-H. 1994. The embryology, reproductive morphology, and systematics of Lecythidaceae. *Mem. New York Bot. Gard.* 71: 1-110.
- Tucker, S. C. & A. Douglas. 1994. Ontogenetic evidence and phylogenetic relationships among basal taxa of legumes. Pp. 11-32 in I. K. Ferguson & S. C. Tucker (editors), *Advances in Legume Systematics*, Vol. 6. Royal Botanic Gardens, Kew.
- Ueda, K., T. Hanyuda, A. Nakano, T. Siuchi, A. Seo, H. Okubo & M. Hotta. 1997. Molecular phylogenetic position of Podostemaceae, a marvelous aquatic flowering plant family. *J. Pl. Res.* 110: 87-92.
- Uesato, S., M. Miyauchi, H. Itoh & H. Inouye. 1986. Biosynthesis of iridoid glucosides in *Galium mollugo*, *G. spurium* var. *echinospermon* and *Deutzia crenata*. Inter-



- mediacy of deoxyloganic acid, loganin and iridodial glucoside. *Phytochemistry* 25: 2515-2521.
- Ukraintseva, V. V. 1993. Pollen morphology of the family Cistaceae in relation to its taxonomy. *Grana, Suppl.* 2: 33-36.
- Veldkamp, J. F. 1984. *Berberidopsis* (Flacourtiaceae) in Australia. *Blumea* 30: 21-29.
- Vestal, P. A. 1937. The significance of comparative anatomy in establishing the relationship of the Hypericaceae to the Guttiferae and their allies. *Philipp. J. Sci.* 64: 199-252.
- Vijayaraghavan, M. R. & U. Dhar. 1976. *Scytopetalum tieghemii*—Embryologically unexplored taxon and affinities of the family Scytopetalaceae. *Phytomorphology* 26: 16-22.
- Vliet, G. J. C. M. van & P. Baas. 1984. Wood anatomy and classification of the Myrtales. *Ann. Missouri Bot. Gard.* 71: 783-800.
- Vogel, C. 1986. *Phytoserologische Untersuchungen zur Systematik der Euphorbiaceae; Beiträge zur intrafamiliären Gliederung und zu Beziehungen im extrafamiliären Bereich.* *Diss. Bot.* 98: 1-124.
- Walia, K. & R. N. Kapil. 1965. Embryology of *Frankenia* Linn. with some comments on the systematic position of the Frankeniaceae. *Bot. Not.* 118: 412-429.
- Walker, J. W. & A. G. Walker. 1984. Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. *Ann. Missouri Bot. Gard.* 71: 464-521.
- Warburg, O. 1894. Flacourtiaceae. Pp. 1-56 in A. Engler & K. Prantl (editors), *Die natürlichen Pflanzenfamilien*. 1st ed., Vol. 6a. Engelmann, Leipzig.
- Whalen, M. A. 1987. Wood anatomy of the American frankenias (Frankeniaceae): Systematic and evolutionary implications. *Amer. J. Bot.* 74: 1211-1223.
- Williams, S. E., V. A. Albert & M. W. Chase. 1994. Relationships of Droseraceae: A cladistic analysis of *rbcl* sequence and morphological data. *Amer. J. Bot.* 81: 1027-1037.
- Williamson, P. S. & E. L. Schneider. 1993. Cabombaceae. Pp. 157-161 in K. Kubitzki (editor), *The Families and Genera of Vascular Plants*, Vol. 2. Springer, Berlin.
- Wilson, C. L. 1965. The floral anatomy of the Dilleniaceae. 1. *Hibbertia* Andr. *Phytomorphology* 15: 248-274.
- Wojciechowska, B. 1969. Seed morphology and anatomy of some *Helianthemum* species. *Monogr. Bot.* 29: 121-135.
- Woon, C. & H. Keng. 1979. Stamens of the Dipterocarpaceae. *Gard. Bull. Singapore* 32: 1-51.
- Wu, C.-Y. & K. Kubitzki. 1993. Circaeasteraceae. Pp. 288-289 in K. Kubitzki (editor), *The Families and Genera of Vascular Plants*, Vol. 2. Springer, Berlin.
- Xiang Q.-Y., D. E. Soltis, D. R. Morgan & P. S. Soltis. 1993. Phylogenetic relationships of *Cornus* L. sensu lato and putative relatives inferred from *rbcl* sequence data. *Ann. Missouri Bot. Gard.* 80: 723-734.
- Yoffe, M. D. 1962. The embryology of *Trochodendron aralioides* Sieb. et Zucc. *Trudy Bot. Inst. Komarova Akad. Nauk S.S.S.R.*, Ser. 7. *Morfol. Anat. Rast.* 5: 250-259. [In Russian.]
- Zenk, M. H., M. Fürbringer & W. Steglich. 1969. Occurrence and distribution of 7-methyljuglone and plumbagin in the Droseraceae. *Phytochemistry* 8: 2199-2200.
- Zhang, Z.-Y. 1987. A study on the pollen morphology of Actinidiaceae and its systematic position. *Acta Phytotax. Sin.* 25: 9-23. [In Chinese.]
- Zurawski, G., B. Perrot, W. Bottomley & P. R. Whitfeld. 1981. The structure of the gene for the large subunit of ribulose-1,5-bisphosphate carboxylase from spinach chloroplast DNA. *Nucl. Acids Res.* 14: 3251-3270.
- Zweifel, R. 1939. Cytologisch-embryologische Untersuchungen an *Balanophora abbreviata* Blume und *Balanophora indica* Wall. *Vierteljahrsschr. Naturf. Ges. Zürich* 84: 245-306.









Appendix 1. Continued.

Table with 28 columns representing botanical characteristics (e.g., endo, emb, emb, etc.) and 55 rows listing plant families (e.g., 1. Ceratophyllaceae, 2. Chloranthaceae, etc.). The data is presented in a grid format with characters like '0', '1', '2', '3', etc., in each cell.















Appendix 1. Continued.

Table with 110 rows (12-110) and columns for 12 morphological characters. Row 12 lists 'clitell. matts'. Each row contains a 12-character code (e.g., '11111111111111') followed by the name of a plant family (e.g., 'Consoeciniaceae'). The characters are: 1: endi. emb; 2: endi. emb; 3: endi. emb; 4: endi. emb; 5: endi. emb; 6: endi. emb; 7: endi. emb; 8: endi. emb; 9: endi. emb; 10: endi. emb; 11: endi. emb; 12: endi. emb.





















Appendix 2. Taxon circumscriptions.

1) Ceratophyllaceae 2) Chloranthaceae 3) Nymphaeaceae 4) Amborellaceae 5) Austrobaileyaceae 6) Illiciales (Schisandraceae, Illiciaceae) 7) Winterales (Canellaceae, Winteraceae) 8) Monocotyledons 9) Aristolochiaceae (Saururaceae, Piperaceae, Aristolochiaceae, Lactoridaceae) 10) Laurales (Calycanthaceae, Monimiaceae, Hernandiaceae, Gyrostemonaceae, Lauraceae; Trimeniaceae are not included in this study) 11) Myristicaceae 12) Annonales (Eupomatiaceae, Annonaceae) 13) Magnoliales (Himantandraceae, Degeneriaceae, Magnoliaceae) 14) Ranunculidae (Menispermaceae, Lardizabalaceae, Circaeasteraceae, Kingdoniaceae, Hydrastidaceae, Ranunculaceae, Berberidaceae, Papaveraceae) 15) Eupteleaceae 16) Platanaceae 17) Nelumbonaceae 18) Trochodendrales (Tetracentraceae, Trochodendraceae) 19) Proteaceae 20) Buxaceae 21) Sabiaceae 22) Didymelaceae 23) Myrothamnaceae 24) Berberidopsidaceae (*Berberidopsis*, *Streptothamnus*) 25) Gunneraceae 26) Rhabdodendraceae 27) Simmondsiaceae 28) Caryophyllales (Chenopodiaceae, Amaranthaceae, Caryophyllaceae, Nyctaginaceae, Phytolaccaceae, Achatocarpaceae, Aizoaceae, *Giesekia*, Portulacaceae, Basellaceae, Cactaceae, Didiereaceae) 29) Asteropeiceae 30) Plumbaginaceae 31) Polygonaceae 32) Dioncophyllaceae 33) Angicostyladaceae 34) Nepenthaceae 35) Droseraceae 36) Tamaricaceae 37) Frankeniaceae 38) Hamamelidales (Atingiaceae, Cercidiphyllaceae, Daphniphyllaceae, Hamamelidaceae) 39) Dilleniaceae 40) Vitaceae 41) Eucryphiaceae 42) Brunelliaceae 43) Cunoniales (Cunoniaceae, Davidsoniaceae, Baueraceae) 44) Paoniaceae 45) Cephalotaceae 46) Grassulaceae 47) Saxifragales s. str. (Grossulariaceae, Haloragaceae, Penthoraceae, Saxifragaceae; without Vahlaceae, Greyiaceae, Francoaceae, Parnassiaceae, and Lepuropetalaceae) 48) Staphyleaceae 49) Elaeagnaceae 50) Rosaceae 51) Rhmannaceae 52) Faganeae (Nothofagaceae, Fagaceae, Balanopaceae, Betulaceae, Myricaceae, Casuarinaceae, Rhoipteleaceae, Juglandaceae) 53) Cucurbitales (Datiaceae, Begoniaceae, Cucurbitaceae) 54) Coriariaceae 55) Urticales (Ulmaceae, Moraceae, Cecropiaceae, Cannabaceae, Urticaceae) 56) Crossosomataceae 57) Connaraceae 58) Oxalidaceae 59) Stachyuraceae 60) Geissolomataceae 61) Geraniaceae 62) Melianthaceae 63) Fabaceae 64) Surianaceae 65) Polygalaceae 66) Rhizophoraceae 67) Zygophyllaceae (incl. Balanitaceae; without Nitriariaceae and Peganaceae) 68) Vochysiaceae 69) Myrtales (Myrtaceae, Combretaceae, Melastomataceae, Punicaceae, Lythraceae, Onagraceae, Trapaceae) 70) Rutales (Anacardiaceae, Simaroubaceae without Picramnioideae and Alvaradooideae, Rutaceae, Meliaceae, Cneoraceae) 71) Sapindales (Aceraceae, Hippocastaneaceae, Sapindaceae) 72) Celastrales (Goupiaceae, Celastraceae, Stackhousiaceae) 73) Irvingiaceae 74) Violaceae 75) Flacourtiaceae (Flacourtiaceae, *Oncoba*, Homalieceae, Scolopieae (without *Banara*), Cascarieae;

without *Aphloia*, *Soyauxia*; latter two taxa not included in the study) 76) Kiggelariaceae [Flacourtiaceae with cyclopentenyl cyanogenic compounds (Erythrospermoideae, Pangieae, Kiggelariaceae)] 77) Salicaceae 78) Elaeocarpaceae (without *Muntingia*, latter taxon not included in the study) 79) Moringaceae 80) Caricaceae 81) Passiflorales (Passifloraceae incl. Paropsiaceae) 82) Euphorbiales (Euphorbiaceae s.l., Pandaceae) 83) Capparales (Bataceae, Gyrostemonaceae, Koerberliniaceae, Resedaceae, Tovariaceae, Capparaceae, Brassicaceae) 84) Tropaeolaceae 85) Salvadoraceae 86) Caryocaraceae 87) Ochneaceae 88) Medusagynaceae 89) Malpighiaceae 90) Linales s. str. (Hugoniaceae, Linaceae) 91) Clusiaceae (incl. Hypericaceae) 92) Bonnetiaceae 93) Elatinaceae 94) Quiinaeae 95) Chrysobalanaceae 96) Dichapetalaceae 97) Trigoniaceae 98) Erythroxylaceae 99) Sphaerosepalaceae 100) Thymelaeaceae 101) Dipterocarpaceae 102) Sarcolaenaceae 103) Bixaceae 104) Cochlospermaceae 105) Cistaceae 106) Malvales s. str. (Tiliaceae, Sterculiaceae, Bombacaceae, Malvaceae) 107) Strasburgeriaceae 108) Podostemaceae 109) Bruniaceae 110) Balanophoraceae 111) Santalales (Olacaceae, Opiliaceae, Santalaceae, Loranthaceae, Viscaceae, Eremolepidaceae) 112) Aextoxicaceae 113) Paracryphiaceae 114) Pentaphylaceae 115) Oncothecaceae 116) Aquifoliaceae (including *Sphenostemon*) 117) Icacinaceae 118) Balsaminaceae 119) Fouquieriaceae 120) Polemoniaceae 121) Loasaceae 122) Cornales (Alangiaceae, Nyssaceae, Davidiaceae, Mastixiaceae, Cornaceae) 123) Hydrangeaceae 124) Diapensiaceae 125) Scytopetalaceae 126) Lecythidaceae 127) Sapotaceae 128) Ebenaceae 129) Styracaceae 130) Primulales (Myrsinaceae, Theophrastaceae, Primulaceae) 131) Clethraceae 132) Actinidiaceae 133) Sarraceniaceae 134) Ericales (Epacridaceae, Ericaceae, Empetraceae, Pyrolaceae) 135) Marcgraviaceae 136) Cyrillaceae 137) Theaceae (incl. Sladeniaceae) 138) Pittosporaceae 139) Araliales (Araliaceae, Apiaceae) 140) Escalloniaceae 141) Dipsacales (Adoxaceae, Sambucaceae, Caprifoliaceae, Viburnaceae, Dipsacaceae, Valerianaceae) 142) Eucommiales (Eucommiaceae, Garryaceae, Aucubaceae) 143) Gentianales (Loganiaceae, Apocynaceae, Asclepiadaceae, Gentianaceae, Rubiaceae) 144) Scrophulariales (Buddlejaceae, Oleaceae, Bignoniaceae, Pedaliaceae, Martyniaceae, Acanthaceae, Scrophulariaceae, Callitrichaceae, Lentibulariaceae, Orobanchaceae, Verbenaceae, Lamiaceae) 145) Solanales (Convolvulaceae, Boraginaceae, Hydrophyllaceae, Solanaceae, Nolanaceae) 146) Symplocaceae 147) Menyanthaceae 148) Campanulales (Goodeniaceae, Brunoniaceae, Calyceraceae, Campanulaceae, Styliidiaceae, Asteraceae) 149) Akaniaceae 150) Bretschneideraceae 151) Corynocarpaceae 152) Huaceae 153) Krameriaceae 154) Lacistemataceae 155) Leitneriaceae 156) Pellicieraceae 157) Peridiscaceae 158) Plagiopteraceae 159) Scyphostegiaceae 160) Tetrameristaceae 161) Tremandraceae

Appendix 3. Characters and character-states.

Serology

1	serological reaction with <i>Nelumbo</i> antiserum (1. group)	A: absent; C: present
2	serological reaction with <i>Nelumbo</i> antiserum (2. group)	A: absent; C: present
3	serological reaction with <i>Victoria</i> antiserum	A: weak or absent; C: present
4	serological reaction with <i>Saxifragaceae</i> antiserum	A: weak or absent; C: present
5	serological reaction with <i>Hynocarpus</i> antiserum	A: weak or absent; C: present
6	serological reaction with <i>Passiflorales</i> antiserum (1. group)	A: absent; C: present
7	serological reaction with <i>Passiflorales</i> antiserum (2. group)	A: absent; C: present

8	serological reaction with Euphorbiaceae antiserum (1. group)	A: absent; C: present
9	serological reaction with Euphorbiaceae antiserum (2. group)	A: absent; C: present
10	serological reaction with Euphorbiaceae antiserum (3. group)	A: absent; C: present
11	serological reaction with Loasaceae antiserum	A: weak or absent; C: present
12	serological reaction with Sapotaceae antiserum	A: weak or absent; C: present
13	serological reaction with Styracaceae antiserum	A: weak or absent; C: present
14	serological reaction with Primulales antiserum	A: weak or absent; C: present
15	serological reaction with Theaceae antiserum	A: weak or absent; C: present
16	serological reaction with Hydrangeaceae antiserum	A: weak or absent; C: present

## Chemical compounds

17	Al accumulation	A: absent; C: present
18	amides	A: absent; C: present
19	dhurrin	A: absent; C: present
20	proteacin	A: absent; C: present
21	triglochinin	A: absent; C: present
22	taxiphyllin	A: absent; C: present
23	proacacipetalin	A: absent; C: present
24	heterodendrin	A: absent; C: present
25	cardiospermin	A: absent; C: present
26	valine- and isoleucine-derived cyanogenic compounds	A: absent; C: present
27	linamarin	A: absent; C: present
28	lotaustralin	A: absent; C: present
29	linustatin	A: absent; C: present
30	neolinustatin	A: absent; C: present
31	tyrosine-derived cyanogenic compounds	A: absent; C: present
32	prunasin	A: absent; C: present
33	sambunigrin	A: absent; C: present
34	zierin	A: absent; C: present
35	holocalin	A: absent; C: present
36	glucosinolates	A: absent; C: present
37	dihydrosterculic acid	A: absent; C: present
38	acetylenes	A: absent; C: present
39	eleostearic acid	A: absent; C: present
40	myristicin	A: absent; C: present
41	asarone	A: absent; C: present
42	sesquiterpene lactones	A: absent; C: present
43	germacrane-like compounds	A: absent; C: present
44	myoinisitol	A: absent; C: present
45	pinitol	A: absent; C: present
46	quebrachitol	A: absent; C: present
47	deutzioid	A: absent; C: present
48	cantleyoside	A: absent; C: present
49	cyclopentenyl cyanogenic glycosids	A: absent; C: present
50	simmondsin-like compounds	A: absent; C: present
51	austrobailignan	A: absent; C: present
52	kadsurin A	A: absent; C: present
53	eucommin A	A: absent; C: present
54	syringaresinol	A: absent; C: present
55	pinoresinol	A: absent; C: present
56	dihydrocubebin	A: absent; C: present
57	galbacin	A: absent; C: present
58	licarin A	A: absent; C: present
59	veraguensin	A: absent; C: present
60	prodelphinidins	A: absent; C: present
61	ellagic acid	A: absent; C: present
62	methylated ellagic acids	A: absent; C: present
63	stachyurins	A: absent; C: present
64	casuaricitin	A: absent; C: present
65	tellimagrandin I	A: absent; C: present
66	tellimagrandin II	A: absent; C: present
67	pedunculagin	A: absent; C: present
68	geraniins	A: absent; C: present
69	chlorogenic acid	A: absent; C: present
70	gallic acid	A: absent; C: present
71	epigallocatechin-3-gallate	A: absent; C: present
72	flavonoid sulphates	A: absent; C: present



73	afzelechin	A: absent; C: present
74	davidigenin	A: absent; C: present
75	biflavonoids or biflavanoids	A: absent; C: present
76	Oouratea catechins	A: absent; C: present
77	euxanthone	A: absent; C: present
78	norathyriol	A: absent; C: present
79	maclura xanthone	A: absent; C: present
80	benzylisoquinoline alkaloids	A: absent; C: present
81	roemerine	A: absent; C: present
82	anonaine	A: absent; C: present
83	liriodenine	A: absent; C: present
84	protuberberine	A: absent; C: present
85	ancistrocladine	A: absent; C: present
86	camptothecine	A: absent; C: present
87	indole alkaloids	A: absent; C: present
88	iridoid compounds	A: absent; C: present
89	secoloiridoid compounds	A: absent; C: present
90	comin	A: absent; C: present
91	oleanolic acid & derivatives	A: absent; C: present
92	arjunolic acid & derivatives	A: absent; C: present
93	dammaranes	A: absent; C: present
94	cucurbitacins	A: absent; C: present
95	nigracin	A: absent; C: present
96	arbutin	A: absent; C: present
97	naphthoquinones	A: absent; C: present
98	rapanone	A: absent; C: present
99	plumbagin	A: absent; C: present
100	droserone	A: absent; C: present
101	anthraquinones	A: absent; C: present
102	phenanthrenes	A: absent; C: present
103	acetophenones	A: absent; C: present
104	actinidine	A: absent; C: present

Characters at cellular level

105	nitrogen-fixing nodules	A: absent; C: present
106	chromosome number $x = 7$ or $n = 6$ or $n = 8$	A: absent; C: present
107	sieve-tube plastids	A: A: P-type; C: S-type
108	epicuticular leaf waxes stratified	A: absent; C: present
109	epicuticular leaf waxes rod or tube shaped	A: absent; C: present
110	epicuticular leaf waxes arranged in rosettes	A: absent; C: present
111	SiO <sub>2</sub> -bodies in wood or leaf	A: absent; C: present
112	oxalate druses	A: absent; C: present
113	elongate oxalate crystals	A: absent; C: raphides; G: prismatic
114	solitary crystals	A: absent; C: present
115	crystal sand	A: absent; C: present
116	sphaerocrystals	A: absent; C: present
117	myrosine cells	A: absent; C: present
118	oil cells	A: absent; C: present
119	mucilage cavities or cells	A: absent; C: present
120	resinous cavities or cells	A: absent; C: present
121	laticiferous cavities	A: absent; C: present
122	fasciculate or stellate hairs	A: absent; C: present
123	peltate scales	A: absent; C: present
124	dendritic hairs	A: absent; C: present
125	nonglandular 2-5 armed hairs	A: absent; C: present
126	glandular scales	A: absent; C: present

Embryology

127	anther tapetum	A: amoeboid; C: secretory
128	microsporogenesis	A: successive; C: simultaneous
129	pollen organization	A: inaperturate; C: monosulcate; G: triaperturate; T: polyforate
130	type of triaperturate pollen	A: not triaperturate; C: tricolpate or polycolpate; G: tri- or polycolpate; T: triporate
131	polar pollen diameter	A: less than 20 $\mu$ ; C: 20-30 $\mu$ ; G: more than 30 $\mu$
132	triangular pollen	A: absent; C: present
133	triangular pollen, ora deepened	A: absent; C: present

- 134 angulaperturate pollen A: absent; C: present  
 135 sexine texture A: psilate or granulate; C: spinulose; G: reticulate; T: striate  
 136 type of reticulation A: not reticulate; C: finely reticulate; G: coarsely reticulate  
 137 integument number A: bitegmic; C: unitegmic  
 138 integumentary tapetum A: absent; C: present  
 139 nucellus type A: crassinucellar; C: weakly crassinucellar; G: tenuinucellar
- 140 perisperm or nucellus-derived surrounding tissue A: absent; C: present  
 141 endosperm development A: nuclear; C: cellular  
 142 Caryophyllad type of embryogeny A: absent; C: present  
 143 Piperad type of embryogeny A: absent; C: present  
 144 Asterad type of embryogeny A: absent; C: present
- Seed anatomy
- 145 end of ovular or seed vascular bundle A: chalazal; C: beyond chalaza, far from micropyle; G: near micropyle
- 146 aril A: absent; C: present  
 147 pachychalaza A: absent; C: present  
 148 sarcotesta A: absent; C: present  
 149 ruminant endosperm A: absent; C: present  
 150 exotestal hairs or papillae A: absent; C: present  
 151 exotestal palisade A: absent; C: present  
 152 theoid exotesta thickenings A: absent; C: present  
 153 exotesta tanniferous or with brown contents A: absent; C: present  
 154 mesotesta A: unspecialized; C: sclerenchymatous or thickened walls  
 155 endotestal crystals A: absent; C: present; G: undefined  
 156 endotesta A: unspecialized cells; C: elongate cells; G: lignified, not elongate; T: tracheids
- 157 exotegmen A: unspecialized cells or with lobate facets; C: sclerified or tracheidal; G: fibrous or tangentially elongate; T: as palisade layer
- 158 exotegmen with lobate facets A: absent; C: present  
 159 bixoid exotegmen in chalazal region A: absent; C: present  
 160 hypostase A: absent; C: present  
 161 endosperm storage type A: oil or proteins; C: starch; G: arabinose; T: undefined  
 162 endosperm haustoria A: absent; C: present  
 163 embryo size A: less than half seed length; C: bigger than in A, endosperm copious; G: bigger than in A, endosperm scanty; T: no endosperm
- 164 embryo form A: straight; C: curved  
 165 suspensor haustoria A: absent; C: present
- Stem morphology and anatomy
- 166 growth form A: no vine; C: vine or creeping axis  
 167 dispersed vascular bundles A: absent; C: present  
 168 anomalous secondary growth A: absent; C: present  
 169 phloem stratification A: absent; C: present  
 170 wedge-shaped phloem rays A: absent; C: present  
 171 internal phloem A: absent; C: present  
 172 cortical vascular bundles A: absent; C: present  
 173 sclerenchymatous idioblasts in cortex or pericycle A: absent; C: present  
 174 wood parenchyma A: scanty or absent; C: diffuse; G: aggregate  
 175 fiber wall A: thin to moderately thick; C: thick to very thick  
 176 fiber septation A: absent; C: present  
 177 tracheids A: absent; C: present  
 178 libriform fibers A: absent; C: present  
 179 ray-type A: heterogenous type I; C: heterogenous type IIa; heterogenous type IIb; T: other
- 180 homogenous multiseriate rays A: absent; C: present  
 181 rays maximally biseriate A: absent; C: present  
 182 storied wood structure A: absent; C: present  
 183 vested pits in vessel side walls A: absent; C: present  
 184 vessel side pitting A: absent; C: present
- 185 end wall perforation of pit A: circular, only one or two rows; C: scalariform or transitional; G: opposite; T: alternate  
 A: tracheids, no perforation; C: scalariform; G: mixed scalariform and simple; T: simple  
 186 vessel end wall angle A: highly oblique; C: slightly oblique; G: horizontal

- 187 vessel shape in transverse section  
188 vessel aggregation  
189 dendritic pattern of vessels
- Leaf characters
- 190 leaf traces  
191 leaf arrangement  
192 stipules  
193 glands on distal petiole  
194 leaf organization  
195 stoma type  
196 epidermal crystals  
197 mucilaginous epidermis  
198 palmate venation  
199 craspedodromous venation  
200 leaf teeth  
201 salicoid teeth  
202 chloranthoid teeth  
203 kranz structure  
204 leaf sclereids  
205 vein terminating foliar sclereids  
206 foliar tracheoids
- Floral and fruiting characters
- 207 elongated floral base  
208 cortical and axial vascular bundles in floral base  
209 bracts instead of perianth or bract-like perianth  
210 K-C differentiation  
211 petal or tepal aestivation
- 212 number of calyx or tepal organs  
213 high calyx or tepal number
- 214 trimery in calyx or tepals  
215 sepal union  
216 petal number  
217 petal union  
218 scales on upper side of petal  
219 perianth or bract to stamen outline change  
220 variation of isomerous patterns
- 221 trimery in androecium  
222 isomery in androecium and perianth  
223 centripetal polyandry  
224 centrifugal polyandry  
225 polyandry associated with outer stamen pairs  
226 anther to stamen length-ratio  
227 inverted anthers  
228 expanded stamen  
229 connective tip
- 230 valvate anther dehiscence  
231 disk  
232 gynoeceum position
- 233 carpel number I  
234 carpel number II  
235 carpel number III
- 236 ovary to carpel length-ratio  
237 carpel union
- 238 degree of syncarpy  
239 stipitate free carpels or stipitate unicarpellate fruits  
240 stigmatic crest
- A: angular; C: slightly angular; G: oval  
A: more than 85% solitary; C: less than 85% solitary; G: no vessels  
A: absent; C: present  
A: one; C: three; G: more than three  
A: alternate; C: opposite; G: whorled  
A: absent; C: present  
A: absent; C: present  
A: simple; C: pinnate  
A: paracytic or tetracytic; C: encycloctytic; G: other types  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: none; C: four or two; G: five; T: six to ten  
A: absent; C: present  
A: absent; C: present  
A: discontinuous; C: continuous  
A: no isomery; C: haplostemony; G: two or n isomerous or doubled whorls; T: obhaplostemony  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: absent; C: present  
A: more than half; C: less than half  
A: absent; C: present  
A: absent; C: present  
A: not prolonged; C: prolonged not as in G or T; G: membranaceous; T: expanded or massive  
A: absent; C: present  
A: absent; C: present  
A: not antepetalous (or antetepalous); C: antepetalous or antetepalous, not oblique; G: oblique  
A: one; C: two; G: three; T: more than three  
A: three or less; C: four; G: five; T: more than five  
A: five or less; C: six to ten; G: eleven to twenty; T: more than twenty  
A: more than 1:2; C: 1:2 to 1:3; G: less than 1:3  
A: unicarpellate or totally apocarpous; C: ovary partially fused; G: styles free or partially fused; T: styles fully fused  
A: not totally syncarpous; C: totally syncarpous  
A: absent; C: present  
A: absent; C: present

241	placentation	A: marginal or laminar on apocarpous carpels; C: apical; G: axile, free central or basal; T: parietal
242	diffuse placenta	A: absent; C: laminar diffuse; T: protruding diffuse
243	stigma decurrent	A: absent; C: present
244	ovary position	A: superior; C: inferior
245	ovule to carpel number	A: less than one; C: one; G: two; T: more than two
246	ovule curvature	A: orthotropous; C: anatropous or campylotropous
247	micropyle formation	A: outer or both integuments; C: inner integument; G: by the only integument; T: no integuments
248	obturator	A: absent; C: present
249	seed to carpel number	A: less than one; C: one; G: two; T: more than two
250	fruit type	A: dehiscent fruit; C: indehiscent fruit
251	type of dehiscent fruit	A: follicle, pod or ventricidal capsule; C: capsule types other than in A and T; G: septicidal capsule; T: indehiscent fruit or schizocarp
252	central column in fruit	A: absent; C: present

Data errors in non-molecular matrix that could not be corrected

Amborellaceae: character 129, A/C instead of A (we became aware of Sampson, 1993, too late to include this polymorphism); Myristicaceae: character 251, A instead of G; Fabaceae: character 105, C instead of A; Myrtales: character 87, C instead of A

#### Appendix 4. Character definitions.

Characters and character-states requiring further explanation are given below.

##### Characters on cellular level

122	fasciculate or stellate hairs	: definition following Metcalfe & Chalk, 1950
123	peltate scales	: definition following Metcalfe & Chalk, 1950
124	dendritic hairs	: definition following Metcalfe & Chalk, 1950
125	nonglandular 2–5 armed hairs	: definition following Metcalfe & Chalk, 1950
126	glandular scales	: definition following Metcalfe & Chalk, 1950

##### Seed anatomy

152	theoid exotesta thickenings	: exotesta showing thickenings on radial and inner tangential walls, but not on outer tangential walls (cf. Huber, 1991)
159	bixoid exotegmen in chalazal region	: seeds with exotegmen organized as palisade layer, the latter showing a typical inward curving in the chalazal region associated with a hypostase plug differentiated into core and annulus region (see Nandi, 1998a)

##### Stem morphology and anatomy

175	fiber wall	: thin to moderately thick means sum of wall-thickness is smaller than fiber lumen diameter
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##### Leaf characters

199	craspedodromous venation	: secondary venation running into leaf teeth
201	salicoid teeth	: leaf teeth showing a proximally rounded hyaline gland with concave gland body in herbarium specimens; see also Doyle & Hickey, 1975
202	chloranthoid teeth	: definition following Doyle & Hickey, 1975
205	vein terminating foliar sclereids	: definition following Rao, 1991
206	foliar tracheoids	: definition following Rao, 1991

##### Floral and fruiting characters

225	polyandry associated with outer stamen pairs	: definition following Ronse Decraene, 1992
228	expanded stamen	: thecae of anthers widely separated or stamen laminar
230	valvate anther dehiscence	: definition following Endress, 1994d
232	gynoecium position	: defined as antepetalous if one carpel is in line with a median tepal or petal
240	stigmatic crest	: broad, decurrent stigma, deeply furrowed into two parts
242	diffuse placenta	: definition following Endress, 1994a

243 stigma decurrent : stigmatic surface unilaterally running down more than three times the stigma lobe breadth

Appendix 5. Procedures of character-state assignment.

The procedures for assigning character-states to matrix fields are indicated in the overview given below. In characters that are not listed, presence was favored over absence (monocots: presence only favored if occurring in *Acorus*, *Arales*, *Arceales*, or *Alismatidae*; the restriction to the presumed basal monocot clades reduces parallelisms).

Serology

Characters 1–16: strongest serological reaction > [">" means favored]

Chemical compounds

Characters 17–114: Presence of a chemical compound > absence

Characters at cellular level

107 sieve-tube plastids Both types equally >, character-state of presumed basal members > in Winterales, Magnoliales, Laurales

Embryology

127 anther tapetum Both types equally >  
 128 microsporogenesis Both types equally >  
 129 pollen organization Character-state of presumed basal members >  
 130 type of triaperturate pollen Character-state of presumed basal members >  
 131 polar pollen diameter least polar pollen diameter >  
 135 sexine texture Character-state of presumed basal members >  
 136 type of reticulation Character-state of presumed basal members >  
 137 integument number A > C  
 138 integumentary tapetum Character-state of presumed basal members >  
 139 nucellus type A > C > G  
 141 endosperm development Both types equally >

Seed anatomy

145 end of ovular or seed vascular bundle G > C > A  
 154 mesotesta C > A  
 156 endotesta T, G, and C > A  
 157 exotegmen T, G, and C > A  
 161 endosperm storage type All types equally >  
 163 embryo size A > C > G > T  
 164 embryo form A > C

Stem morphology and anatomy

166 growth form Both types equally >  
 168 anomalous secondary growth Character state of presumed basal members >  
 171 internal phloem Character state of presumed basal members >  
 174 wood parenchyma A > C > G  
 175 fiber wall A > C  
 176 fiber septation A > C  
 178 libriform fibers Absence > presence  
 179 ray-type A > C > G > T  
 180 homogenous multiserial rays Character state of presumed basal members >  
 181 rays maximally biserial Character state of presumed basal members >  
 184 vessel side pitting A and C > G > T  
 185 end wall perforation of pit A > C > G > T  
 186 vessel end wall angle A > C > G  
 187 vessel shape in transverse section A > C > G  
 188 vessel aggregation G > A > C

Leaf characters

190 leaf traces Character state of presumed basal members >  
 191 leaf arrangement Character state of presumed basal members >  
 194 leaf organization Both types equally >  
 195 stoma type Character state of presumed basal members >  
 200 leaf teeth Character state of presumed basal members >

Floral and fruiting characters

209 bracts instead of perianth or bract-like perianth Character state of presumed basal members >

210	K-C differentiation	A > C
211	petal or tepal aestivation	Character state of presumed basal members >
212	number of calyx or tepal organs	Character state of presumed basal members >
213	high calyx or tepal number	Character state of presumed basal members >
214	trimery in calyx or tepals	Character state of presumed basal members >
215	sepal union	Absence > presence
216	petal number	Character state of presumed basal members >
217	petal union	Absence > presence
219	perianth or bract to stamen outline change	C > A
220	variation of isomeric patterns	Character state of presumed basal members >
221	trimery in androecium	Character state of presumed basal members >
222	isomery in androecium and perianth	Character state of presumed basal members >
223	centripetal polyandry	Character state of presumed basal members >
224	centrifugal polyandry	Character state of presumed basal members >
226	anther to stamen length-ratio	Character state of presumed basal members >
229	connective tip	T > G and C > A
231	disk	Character state of presumed basal members >
232	gynoecium position	A > C and G
233	carpel number I	Character state of presumed basal members >
234	carpel number II	Character state of presumed basal members >
235	carpel number III	Character state of presumed basal members >
236	ovary to carpel length-ratio	A > C > G
237	carpel union	A > C > G > T
238	degree of syncarpy	A > C
241	placentation	Character state of presumed basal members >
242	diffuse placenta	Character state of presumed basal members >
244	ovary position	A > C
245	ovule to carpel number	T > G > C > A
246	ovule curvature	Character state of presumed basal members >
247	micropyle formation	Character state of presumed basal members >
249	seed to carpel number	T > G > C > A
250	fruit type	Character state of presumed basal members >
251	type of dehiscent fruit	A > C and G > T

## Appendix 6. Sources.

Literature used for taxon delimitations and for finding character-states.

## Taxon delimitations

Albert et al., 1992; Alverson et al., 1994; Baas, 1972, 1975; Carpenter & Dickison, 1976; Chase & Swensen, 1995; Chase et al., 1993, 1995; Conti et al., 1993; Corner, 1976; Cronquist, 1981, 1983; Dahlgren, 1980, 1983; Dahlgren & Clifford, 1982; Dahlgren & Thorne, 1984; Dahlgren et al., 1985; Downie & Palmer, 1994; Duvall et al., 1993b; Engler & Prantl (eds.), 1887-1914, 1924-1995; Fernando et al., 1995; Gadek et al., 1992; Geetha et al., 1993; Gustafsson & Bremer, 1995; Hegnauer, 1962-1994; Huber, 1991; Hutchinson, 1964/1967, 1973; Kolbe & John, 1979a, b; Kron & Chase, 1993; Lemke, 1988; Melchior (ed.), 1964; Miller, 1975; Morgan & Soltis, 1993; Olmstead et al., 1992, 1993; Price & Palmer, 1993; Qiu et al., 1993; Rodman et al., 1993; Savolainen et al., 1994; Soltis et al., 1995b; Sutter & Endress, 1995; Swensen et al., 1994; Takhtajan, 1966, 1987; Thorne, 1983, 1992; van Vliet & Baas, 1984; Xiang et al., 1993

## Serology

Fairbrothers, 1966; Grund & Jensen, 1981; Hillebrand & Fairbrothers, 1966, 1970; Jensen & Greven, 1984; John & Kolbe, 1980; Kolbe & John, 1979a, b; Simon, 1970, 1971; Vogel, 1986

## Chemical compounds

Arora & Metha, 1981; Barron et al., 1988; Bliss et al.,

1968; Bohm & Chan, 1992; Brüning & Wagner, 1978; Crossley & Djerassi, 1962; Deyama et al., 1985; Durant & Zenk, 1974; Filho et al., 1985; Fieser & Chamberlain, 1948; Gibbs, 1974; Gildemeister & Hoffmann, 1956; Harborne, 1969; Harborne & Baxter, 1993; Hayashi et al., 1980; Hegnauer, 1962-1994; Keller, 1982; Lavault & Bruneton, 1980; Le Quesne et al., 1980; Lebreton & Bouchez, 1967; McAlpine et al., 1968; Murai et al., 1985; Rao & Alvarez, 1982; Sethi et al., 1976; Sévenet et al., 1971; Smith et al., 1980; Thieme & Bencke, 1966, 1970; Uesato et al., 1986; Zenk et al., 1969

## Characters on cellular level

Baas, 1972, 1975, 1984; Baas et al., 1979; Behnke, 1975, 1977, 1981, 1985; Carpenter & Dickison, 1976; Cronquist, 1981, 1983; Dickison, 1978, 1981, 1990; Dickison & Baas, 1977; Ditsch & Barthlott, 1994; Ehrendorfer et al., 1984; Engler & Prantl (eds.), 1887-1914, 1924-1995; Fehrenbach & Barthlott, 1988; Franceschi & Horner, 1980; Goldblatt & Dorr, 1986; Goldblatt & Johnson (eds.), 1981/1984/1985/1988/1990/1991/1994; Gottwald & Parmeswaran, 1966, 1967, 1968; Hennig et al., 1994; Huber, 1991; Hutchinson, 1973; Keng, 1962; Metcalfe, 1956, 1962, 1987; Metcalfe & Chalk, 1950, 1988/1989; Miller, 1975; Proctor, 1955; Puff & Weber, 1976; Ricci, 1957; Schmid, 1964; Solereder, 1899/1908; Solereder & Meyer, 1928; Sprent & McKey (eds.), 1994; Theisen & Barthlott, 1994

## Embryology

Baas, 1972; Barth, 1965; Batygina et al., 1985a, b, c; Bhandari, 1971; Boesewinkel, 1985, 1994; Boesewinkel

& Bouman, 1980; Carpenter & Dickison, 1976; Chiarugi, 1925; Chiarugi & Francini, 1930; Chopra & Harjinder, 1965; Corner, 1976; Cronquist, 1981; Davis, 1966; Dickison, 1979, 1981, 1986, 1990; Dickison & Baas, 1977; Dickison et al., 1982; Endress, 1993a, b, c; Erdtman, 1952, 1958; Gavrilova, 1993; Gutzwiller, 1961; van Heel, 1967, 1984; Heo & Tobe, 1994; Hildeux & Ferguson, 1976; Huang Tseng-Chieng, 1972; Huber, 1991, 1993; Huynh, 1969; Jäger-Zürn, 1966; Johri, 1970; Johri & Kak, 1954; Johri et al., 1967, 1992; Kamelina et al., 1981, 1983; Kapil & Bhatnagar, 1991; Kapil & Maheshwari, 1965; Kaur, 1969; Keating, 1972, 1975; Köhler, 1994; Kubitzki, 1993a, b, c; Les, 1988, 1993; Maguire & Ashton, 1980; Mauritzon, 1935, 1936; Maury et al., 1975; Melchior (ed.), 1964; Netolitzky, 1926; Philipson, 1993; Prance, 1968, 1972; Puff & Weber, 1976; Rutishauser, 1997; Sáenz de Rivas, 1979; Satabié, 1974; Schmid, 1964; Schnarf, 1931; Souèges, 1937; Takhtajan (ed.), 1985/1988/1991; Tang, 1994; Thanikaimoni, 1986; Tobe & Peng, 1990; Tobe & Raven, 1995; Todzia, 1993; Tsou, 1974; Ukraintseva, 1993; Vijayaraghavan & Dhar, 1976; Walia & Kapil, 1965; Walker & Walker, 1984; Williamson & Schneider, 1993; Wu Cheng-Yih & Kubitzki, 1993; Yoffe, 1962; Zhang Zhi-Yu, 1987

#### Seed anatomy

Baas, 1972; Blank, 1939; Boesewinkel, 1985, 1994; Boesewinkel & Bouman, 1980; Corner, 1976; Cronquist, 1981; Dickison & Baas, 1977; Endress, 1980, 1987; Engler & Prantl (eds.), 1887-1914, 1924-1995; van Heel, 1967; Huber, 1991; Keng, 1962; Mc Nair, 1930; Netolitzky, 1926; Seubert, 1993; Takhtajan (ed.), 1985/1988/1991; Thanikaimoni, 1986; Tobe & Peng, 1990; Tobe & Raven, 1995; Wojciechowska, 1969

#### Stem morphology and anatomy

Baas, 1969, 1972, 1975, 1984; Baas & Werker, 1981; Baas et al., 1979; Bailey, 1980; Bailey, 1933, 1957; Bailey & Swami, 1948; Baretta-Kuipers, 1976; Berg, 1977; Blank, 1939; Canright, 1955; Carlquist, 1964, 1976, 1977, 1981, 1984a, b, c, d, 1988a, b, 1990, 1993; Carlquist & Hoekman, 1985; Carpenter & Dickison, 1976; Cronquist, 1981; Dahlgren & Thorne, 1984; Dechamps, 1979-1985; Decker, 1966; Den Outer & Vooren, 1980; Dickison, 1969, 1978, 1981, 1986, 1990; Dickison & Baas, 1977; Endress, 1993a, b, c; Garratt, 1933; Gottwald & Parameswaran, 1966, 1967, 1968; Gutzwiller, 1961; Heimsch, 1942; Hekking, 1988; Huber, 1993; Humphrey, 1935; Ilic, 1991; Keefe & Moseley, 1978; Keng, 1962; Kessler, 1993; Kribs, 1935; Kubitzki, 1993a, b, c; Les, 1993; Maguire & Ashton, 1980; Maguire et al., 1972; Mengena, 1982; Metcalfe, 1952, 1956, 1962, 1987; Metcalfe & Chalk, 1950, 1988/1989; Meylan & Butterfield, 1978; Miller, 1975; Philipson, 1993; Piccioli, 1901; Prance, 1972; Prance & da Silva, 1973; Puff & Weber, 1976; Record, 1933; Schmid, 1964; Schweingruber, 1990; Shiklina, 1977; Solereder, 1899/1908; Takahashi, 1985; Takhtajan, 1966; Taylor, 1972; Tomlinson, 1961; Vestal,

1937; van Vliet & Baas, 1984; Whalen, 1987; Williamson & Schneider, 1993

#### Leaf characters

Arber, 1925; Baas, 1969, 1972, 1975, 1984; Baas et al., 1979; Bedell, 1981; Berg, 1977; Blank, 1939; Canright, 1955; Capuron, 1974; Carpenter & Dickison, 1976; Crane, 1989; Crane et al., 1993; Cronquist, 1981; Cuatrecasas, 1985; Dahlgren & Thorne, 1984; Dickison, 1978, 1981, 1990; Dickison & Baas, 1977; Dilcher & Crane, 1984; Engler & Prantl (eds.), 1887-1914, 1924-1995; Heywood (ed.), 1978; Hufford, 1992; Humphrey, 1935; Hutchinson, 1964/1967, 1973; Keng, 1962; Klucking, 1992; Kostermans, 1985; Les, 1993; Levin, 1986; Maguire & Ashton, 1980; Melchior (ed.), 1964; Metcalfe, 1956, 1962, 1987; Metcalfe & Chalk, 1950, 1988/1989; Prance, 1972; Prance & da Silva, 1973; Puff & Weber, 1976; Rao, 1991; Schmid, 1964; Sinnott, 1914; Takhtajan, 1966; Thanikaimoni, 1986; Tomlinson, 1961

#### Floral and fruiting characters

Airy Shaw, 1951; Baas, 1972; Baas et al., 1979; Baillon, 1873; Batygina et al., 1985a, b, c; Bausch, 1938; Bayer & Hoppe, 1990; Berg, 1977; van Beusekom, 1971; Blank, 1939; Bureau, 1958; Brizicky, 1964; Carpenter & Dickison, 1976; Corner, 1946; Crane et al., 1993; Cronquist, 1981, 1983; Cuatrecasas, 1985; Dahlgren & Rao, 1969; Dahlgren et al., 1985; Dickison, 1969, 1978, 1981, 1986, 1990; Dickison & Baas, 1977; Dilcher & Crane, 1984; Drinnan et al., 1991; Drude, 1891a, b; Endress, 1986, 1989, 1993a, b, c, 1994a, b, c, d; Endress & Stumpf, 1991; Engler, 1930; Engler & Prantl (eds.), 1887-1914, 1924-1995; Friis, 1984; Gagnepain et al. (eds.), 1907-1942; Gore, 1935; Gutzwiller, 1961; Haber, 1959, 1961, 1966; van Heel, 1966, 1967, 1984; Heinig, 1951; Hekking, 1988; Heo & Tobe, 1994; Heywood (ed.), 1978; Hirmmer, 1918; Huber, 1991, 1993; Hufford, 1992; Hufford & Endress, 1989; Hutchinson, 1964/1967, 1973; Jäger-Zürn, 1966; Janchen, 1909; Johri et al., 1992; Kamelina et al., 1981; Kamelina et al., 1983; Kanis, 1968; Keating, 1972; Keng, 1962; Kessler, 1993; Kobuski, 1951; Kostermans, 1985; Kubitzki, 1993a, b, c; Leenhouts, 1956; Les, 1993; Letouzey, 1961; Maguire & Ashton, 1980; Martius (ed.), 1840-1906; Melchior (ed.), 1964; Metcalfe, 1956; Payer, 1857; Philipson, 1993; Pilger, 1925a, b; Prance, 1972; Prance & da Silva, 1973; Puff & Weber, 1976; Rendle et al., 1921; Ronse Decraene, 1989, 1992; Ronse Decraene & Smets, 1992; Rutishauser, 1997; Sandwith, 1962; Sattler, 1973; Saunders, 1937; Saunders, 1937-1939; Schaeppi, 1953; Schmid, 1964; Stearn, 1946; Sutter & Endress, 1995; Takhtajan, 1966, 1987; Thanikaimoni, 1986; Tobe & Peng, 1990; Tobe & Raven, 1995; Todzia, 1993; Veldkamp, 1984; Williamson & Schneider, 1993; Wilson, 1965; Woon & Keng, 1979; Wu Cheng-Yih & Kubitzki, 1993

Hostplants of fungi and butterflies (not included in computation)

Ackery, 1988, 1991; DeVries, 1987; Farr et al., 1989; Pierre, 1984

Appendix 7. Table of *rbcL* taxa.Table of taxa samples for *rbcL*. These are arranged alphabetically by families (mostly according to Cronquist, 1981).

Species	Family	Voucher/source	Literature citation§	GenBank accession
<i>Actinidia chinensis</i> Planch.	Actinidiaceae	Kron 2117, NCU	Albert et al., 1992	L01882
<i>Aextoxicon punctatum</i> Ruiz & Pav.	Aextoxiaceae	Chase 959, K	this paper	
<i>Akanta bidwillii</i> (Hoge) Mabbl.	Akaniaceae	Fernando & Quinn 21606, UNSW	Gadek et al., 1992	L12568
<i>Amborella trichopoda</i> Baill.	Amborellaceae	Thien 500, NO	Qiu et al., 1993	L12628
<i>Ancistrocladus korupensis</i> D. W. Thomas & Gereau	Ancistrocladaceae	Gereau et al. 5203, MO	this paper	
<i>Asimina triloba</i> (L.) Dunal	Annaceae	Qiu 15, NCU	Qiu et al., 1993	L12631
<i>Ilex crenata</i> Thunb.	Aquifoliaceae	Chase 119, NCU	Albert et al., 1992	L01928
<i>Acorus callamus</i> L.	Araceae	French 232, CH	Duvall et al., 1993a	M91625
<i>Aralia spinosa</i> L.	Araliaceae	Plunkett 1371, WS	Chase et al., 1993	L11166
<i>Asarum canadense</i> L.	Aristolochiaceae	none	Chase et al., 1993	L14290
<i>Asteropeia microsteira</i>	Asteropeiaceae	Cireyrd s.n., K	this paper	
<i>Austrobaileya scandens</i> C. T. White	Austrobaileiaceae	Qiu 90030, NCU	Qiu et al., 1993	L12632
<i>Impatiens capensis</i> Merb.	Balsaminaceae	Chase 114, NCU	Chase et al., 1993	
<i>Mahonia bealei</i> (Fortune) Carr.	Berberidaceae	Qiu 74, NCU	Qiu et al., 1993	L12657
<i>Berberidopsis corallina</i> Hook. f.	Berberidopsidaceae	Chase 555, K	this paper	
<i>Bixa orellana</i> L.	Bixaceae	Alverson s.n., WISC	this paper	
<i>Brassica campestris</i> L.	Brassicaceae	unknown	Olmstead et al., 1992	
<i>Bretschneidera sinensis</i> Hemsf.	Bretschneideraceae	Leu & Lin 726, WIS	Chase et al., 1993	M95753
<i>Berzella lanuginosa</i> (L.) Brongn.	Bruniaceae	Price s.n., Ind.	Olmstead et al., 1993	L14391
<i>Pachysandra procumbens</i> Michx.	Buxaceae	Chase 207, NCU	Chase et al., 1993	
<i>Chimonanthus praecox</i> (L.) Link	Calycanthaceae	Qiu 62, NCU	Qiu et al., 1993	L12639
<i>Lobelia erinus</i> L.	Campanulaceae	Jansen 989, MICH	Albert et al., 1992	L01931
<i>Canella winterana</i> (L.) Gaertn.	Canelaceae	Qiu 90017, NCU	Qiu et al., 1993	
<i>Viburnum acerifolia</i> L.	Caprifoliaceae	Jansen 910, MICH	Olmstead et al., 1992	L01959
<i>Carica papaya</i> L.	Caricaceae	Wisconsin BG	Rodman et al., 1993	M95671
<i>Caryocarp glabrum</i> Pers.	Caryocaraceae	Mori 22997 NY	this paper	
<i>Euonymus alatus</i> (Thunb.) Siebold	Celastraceae	Chase 137, NCU	Chase et al., 1993	L13184
<i>Cephalotus follicularis</i> Labill.	Cephalotaceae	Chase 147, NCU	Albert et al., 1992	L01894
<i>Ceratophyllum demersum</i> L.	Ceratophyllaceae	Les s.n., CONN	Les et al., 1991	M77030
		Qiu 91027, NCU	Qiu et al., 1993	
<i>Spinacia oleracea</i> L.	Chenopodiaceae	unknown	Zarawski et al., 1981	J01443
<i>Chloranthus japonicus</i> Siebold	Chloranthaceae	Chase 204, NCU	Qiu et al., 1993	L12640
<i>Chrysobalanus icaco</i> L.	Chrysobalanaceae	Fairchild Trop. G 76-311	Morgan & Soltis, 1993	L11178
<i>Helianthemum grandiflorum</i> (Scop.) DC.	Cistaceae	Chase 525, K	this paper	



Species	Family	Voucher/source	Literature citation§	GenBank accession
<i>Clatira alnifolia</i> L.	Clethraceae	Kron 1884, NCU	Kron & Chase, 1993	L12609
<i>Clusia gundlachii</i> Stahl	Clusiaceae	Chase 341, NCU	Fay et al., 1997	Z75673
<i>Quisqualis indica</i> L.	Combretaceae	W. R. Anderson s.n., MICH	Albert et al., 1992	L01948
<i>Gonarus conchocarpus</i> F. Muell.	Connaraeae	Uhl 601, BH	Morgan et al., 1994	U06798
<i>Coriaria myrifolia</i> L.	Coriariaceae	Chase 245, NCU	Albert et al., 1992	L01897
<i>Cornus walteri</i> Wangerin	Cornaceae	Arnold Arb. 414-67-A	Xiang et al., 1993	L11220
<i>Corynocarpus laetigata</i> J. R. Forst. & G. Forst.	Corynocarpaeeae	no voucher	this paper	
<i>Dudleya viscidula</i> (S. Watson) Moran	Crassulaceae	Huntington BG 62801	Morgan & Soltis, 1993	L11182
<i>Crossosoma californicum</i> Nutt.	Crossosomataceae	Rancho Santa Ana BG	Morgan & Soltis, 1993	L11179
<i>Cucurbita pepo</i> L.	Cucurbitaceae	none	Chase et al., 1993	L21938
<i>Ceratopetalum gummiferum</i> Small	Caunotiaceae	Keller 2135, CAS	Albert et al., 1992	L01895
<i>Cyrilla racemiflora</i> L.	Cyrtillaceae	Kron s.n., NCU	Albert et al., 1992	L01900
<i>Diapensia lapponica</i> L.	Diapensiaceae	Hills 89018, NCU	Kron & Chase, 1993	L12612
<i>Dichapetalum macrocarpon</i> Engl.	Dichapetalaceae	Fison s.n., K	this paper	
<i>Didymelea perrieri</i> Leandri	Didymelaceae	Leandri s. n., MO	this paper	
<i>Dillenia indica</i> L.	Dilleniaceae	Chase 234, NCU	Albert et al., 1992	L01903
<i>Triphyophyllum pelatum</i> (Hutchinson & Dalziel) Airy Shaw	Dionocophyllaceae	Chase 663, K	this paper	
<i>Shorea zeylanica</i> (Thwaites) Ashton	Dipterocarpaceae	Dayanandan D6, GF	Chase et al., 1993	
<i>Drosera binata</i> Labill.	Droseraceae	Williams DA1, IVC	Williams et al., 1994	L01911
<i>Diospyros virginiana</i> L.	Ebenaceae	Kron 3004, NCU	Kron & Chase, 1993	L12613
<i>Hippophae salicifolia</i> Elaeocarpaceae	Elaeagnaceae	Chase 856, K	this paper	
<i>Erica australis</i> L.	Ericaceae	Quinn s.n., UNSW	this paper	
<i>Escallonia coquimbensis</i> Remy	Escalloniaceae	RBG Edinburgh 781912	Chase et al., 1993	L13183
<i>Eucommia ulmoides</i> Oliv.	Eucommiaceae	U. Calif. BG 521333	Morgan & Soltis, 1993	L11183
<i>Eucyphia lucida</i> Druce	Eucyphiaceae	Qiu 91024, NCU	Albert et al., 1992	L01917
<i>Jatropha interregina</i> Jacq.	Euphorbiaceae	Strybing Arb. 86-0250	Albert et al., 1992	L01918
<i>Euptelea polyandra</i> Siebold & Zucc.	Eupteleaceae	Fairchild Trop. G 63769A	this paper	
<i>Medicago sativa</i> L.	Fabaceae	Qiu 90026, NCU	Qiu et al., 1993	L12645
<i>Nothofagus dombeyi</i> (Mithb.) Oerst.	Fagaceae	unknown	Aldrich et al., 1986	
<i>Ptilothysis sinensis</i> Hook. f.	Flacourtiaceae	U Washington BG	Chase et al., 1993	L13350
<i>Frankenia pulverulenta</i> L.	Frankeniaceae	K. Wurdack s.n., NCU	this paper	
<i>Fouquieria columnaris</i> Kellogg	Fouquieriaceae	Collenette 693, K	this paper	
		U of California, Irvine, Arb.	Morton et al., 1997	

## Appendix 7. Continued.

Species	Family	Voucher/source	Literature citation§	GenBank accession
<i>Trichadenia zeylanica</i> Thwaites	Kiggeliaceae	Chase 1289, K	this paper	
<i>Geissoloma marginatum</i> (L.) A. Juss.	Geissolomataceae	unknown	Savolainen, unpubl.	L14398
<i>Gentiana procer</i> Holm	Gentianeaceae	none	Olmstead et al., 1993	L01920
<i>Gerranium grandiflorum</i> Gilib.	Geraniaceae	Price s.n., IND	Albert et al., 1992	
<i>Gunnera hamiltonii</i> Kirk ex W. S. Ham.	Gunneraceae	Chase 562, K	this paper	L01922
<i>Hamamelis mollis</i> Oliv.	Hamamelidaceae	Qiu 91035, NCU	Albert et al., 1992	
<i>Hua gabonii</i> Pierre ex De Wild.	Huaceae	Wieringa 3177, WAG	this paper	L11187
<i>Hydrangea macrophylla</i> Torr.	Hydrangeaceae	Morgan 2150, WS	Morgan & Soltis, 1993	
<i>Icacina manni</i> Oliv.	Illiciaceae	van Setten 460, WAG	this paper	L12652
<i>Illicium parviflorum</i> Michx. ex Vent.	Illiciaceae	Qiu 83, NCU	Qiu et al., 1993	
<i>Irvingia malayana</i> Oliv. ex Benn.	Irvingiaceae	Simpson 2638, K	Fernando et al., 1995	
<i>Koerberlinia spinosa</i> Zucc.	Koerberliniaceae	Al-Shehbaz s.n., WIS	Rodman et al., 1993	L14600
<i>Krameria lanceolata</i> Torr.	Krameriaceae	Simpson 88-05-1-1, MICH	Chase et al., 1993	
<i>Lacistema aggregatum</i> Rusby	Lacistemataceae	Pennington et al. 583, K	this paper	
<i>Leitneria floridana</i> Chapm.	Leitneriaceae	Qiu 91033, NCU	Chase et al., 1993	
<i>Gourouputa guianensis</i> Aublet	Lecythidaceae	RBG Kew 1960-43401	Morton et al., 1997	
<i>Linum perenne</i> L.	Linaceae	Chase 111, NCU	Fay et al., 1997	Z75681
<i>Magnolia hypoleuca</i> Siebold & Zucc.	Magnoliaceae	Qiu 24, NCU	Qiu et al., 1993	L12655
<i>Byrsionima crassifolia</i> (L.) Kumph	Malpighiaceae	Fairchild Trop. G 81680, MICH	Albert et al., 1992	L01892
<i>Gossypium robinsonii</i> F. Muell.	Malvaceae	Wendell s.n., ISC	Chase et al., 1993	L13186
<i>Marcgravia rectiflora</i> Triana & Planch.	Marcgraviaceae	Chase 331, NCU	this paper	
<i>Medusagynne oppositifolia</i> Baker	Medusagynaceae	Chase 670, K	Fay et al., 1997	Z75670
<i>Bersania lucens</i> Szyszyl.	Meliastriaceae	Chase 1125, K	this paper	
<i>Menyanthes trifoliata</i> L.	Menyanthaceae	none	Olmstead et al., 1993	L14006
<i>Morus alba</i> L.	Moraceae	none	Albert et al., 1992	L01933
<i>Moringa oleifera</i> Lam.	Moringaceae	Illis 30501, WIS	Rodman et al., 1993	L11359
<i>Knema latericia</i> Elmer	Myrsinaceae	Qiu 91041, NCU	Qiu et al., 1993	L12653
<i>Maesa myrsinoides</i> Leveille	Myrsinaceae	Chase 309, K	this paper	
<i>Myrothamnus</i> sp.	Myrothamnaceae	Hoot s.n., F	this paper	
<i>Nelumbo lutea</i> (Willd.) Pers.	Nelumbonaceae	Les s.n., CONN	this paper	M77032
<i>Nepenthes adata</i> Blanco	Nepenthaceae	Qiu 91028, NCU	Qiu et al., 1993	L01936
<i>Nymphopha odorata</i> Alton	Nymphophaeaceae	Chase 145, NCU	Albert et al., 1992	M77035
		Les s.n., CONN	Les et al., 1991	
		Qiu 91029, NCU	Qiu et al., 1993	

Species	Family	Voucher/source	Literature citation§	GenBank accession
<i>Ochna multiflora</i> DC.	Ochnaceae	Chase 229, NCU	Chase et al., 1993	L11205
<i>Schoepfia schreberii</i> J. F. Gmel.	Oleaceae	Nickrent 2599, I.L.	Morgan & Soltis, 1993	L01938
<i>Oxalis dillenii</i> Jacq.	Oxalidaceae	Price s.n., IND	Albert et al., 1992	L13187
<i>Paeonia tenuifolia</i> L.	Paeoniaceae	Kron 2115, NCU	Chase et al., 1993	L01940
<i>Passiflora quadrangularis</i> L.	Passifloraceae	Kron 3000, NCU	this paper	L11202
<i>Pelliciera rhizophora</i> Planchon & Triana	Pellieraceae	Pennington et al. 586, K	Morgan & Soltis, 1993	L01943
<i>Pitosporum japonicum</i> Hort. ex C. Presl	Pitosporaceae	Rieseberg s.n., RSA	this paper	M77701
<i>Plagiopteron suavelens</i> Griff.	Plagiopteridaceae	Chase 1335, K	this paper	L01945
<i>Platanus occidentalis</i> L.	Platanaceae	Qui P90005, NCU	Albert et al., 1992	M77702
<i>Plumbago capensis</i> Thunb.	Plumbaginaceae	unknown	Giannasi et al., 1992	L11190
<i>Gilia aggregata</i> (Pursh) Spreng.	Polemoniaceae	Chase 970, K	this paper	Z75689
<i>Polygala cruciata</i> L.	Polygalaceae	Chase 155, NCU	Albert et al., 1992	L13189
<i>Rheum × cultorum</i> (Thorsrud & Reisaeter)	Polygonaceae	unknown	Giannasi et al., 1992	U06824
<i>Lambertia inermis</i> R. Br.	Proteaceae	Natl. Trop. BG, Hawaii	Morgan & Soltis, 1993	L12662
<i>Quina pteridophylla</i> (Radlk.) Pries	Quinaceae	Pennington 13846, K	Fay et al., 1997	
<i>Rhabdodendron amazonicum</i> Huber	Rhabdodendraceae	Ribeiro 1187, K	this paper	
<i>Rhamnus cartharticus</i> L.	Rhamnaceae	Chase 100, NCU	Chase et al., 1993	
<i>Rosa woodsii</i> Lindl.	Rosaceae	Soltis & Soltis 2410, WS	Morgan et al., 1994	
<i>Poncirus trifoliata</i> (L.) Raf.	Rutaceae	Chase 117, NCU	Chase et al., 1993	
<i>Sabia</i> sp.	Sabiaceae	Qui 91025, NCU	Chase et al., 1993	
<i>Salix reticulata</i> L.	Salicaceae	Chase 840, K	this paper	
<i>Salvadora persica</i> L.	Salvadoraceae	Verdcourt s.n., K	Savolainen, unpubl.	
<i>Koeleruteria paniculata</i> Laxm.	Sapindaceae	Chase 115, NCU	this paper	
<i>Manilkara zapota</i> (L.) Royen	Sapotaceae	Chase 129, NCU	Albert et al., 1992	L01932
<i>Sarracea flava</i> L.	Sarraceniaceae	Chase 144, NCU	Albert et al., 1992	L01952
<i>Saxifraga integrifolia</i> Hook.	Saxifragaceae	Soltis & Soltis 2253, WS	Morgan & Soltis, 1993	L01953
<i>Scyphostegia borneensis</i> Stapf	Scyphostegiaceae	J. Davis s.n., BH	this paper	
<i>Oubanguia alata</i> Baker f.	Scytotetralaceae	Geneau et al. 5202, K	this paper	L01902
<i>Digitalis purpurea</i> L.	Scrophulariaceae	none	Albert et al., 1992	
<i>Simmondsia chinensis</i> (Link) C. K. Schneider	Simmondsiaceae	Hoot s.n., F	this paper	
<i>Nicotiana tabacum</i> L.	Solanaceae	unknown	this paper	
<i>Rhopalocarpus</i> sp.	Sphaerosepalaceae	Chase 906, K	Lin et al., 1986	
<i>Stachyurus praecox</i> Sieb. & Zucc.	Stachyuraceae	Chase 800, K	this paper	
<i>Staphylea trifoliata</i> Payer	Staphyleaceae	Chase 116, NCU	this paper	
<i>Styrax americana</i> Lam.	Styracaceae	Kron 3002, NCU	Kron & Chase, 1993	L12623

## Appendix 7. Continued.

Species	Family	Voucher/source	Literature citation§	GenBank accession
<i>Symplocos paniculata</i> Miq.	Symplocaceae	Kron 3005, NCU unknown	Kron & Chase, 1993	L12624
<i>Suriana maritima</i> L.	Surianaceae	Chase 252, NCU	Fernando et al., 1995	U07680
<i>Tamarix pentandra</i> Bunge	Tamaricaceae	Qui 90009, NCU	this paper	
<i>Tetacentron sinensis</i> Oliv.	Tetacentraceae	Coode 7925, K	Chase et al., 1993	L12668
<i>Tetramerista</i> sp.	Tetrameristaceae	Chase 1380, K	Morton et al., 1997	
<i>Aquilaria beccariana</i> Tregl.	Thymelaeaceae	none	this paper	
<i>Camellia japonica</i> L.	Theaceae	Chase 179, NCU	Kron & Chase, 1993	L12602
<i>Platytheca verticillata</i> Baill.	Tremandraceae	W. R. Anderson 13656, MICH	Chase et al., 1993	L01944
<i>Trigonon nireu</i> Cambess.	Trigonaceae	Chase 113, NCU	Chase et al., 1993	
<i>Tropaeolum majus</i> L.	Tropaeolaceae	Chase 226, NCU	Price & Palmer, 1993	L14706
<i>Viola sororia</i> Willd.	Violaceae	W. R. Anderson 13660, MICH	Olmstead et al., 1992	L11674
<i>Vitis aestivalis</i> Michx.	Vitaceae	Qui 90016, NCU	Albert et al., 1992	L01960
<i>Qualea</i> sp.	Vochysiaceae	W. R. Anderson s.n., MICH	Olmstead et al., 1992	U02730
<i>Drimys winteri</i> J. R. Forst. & G. Forst.	Winteraceae		Albert et al., 1992	L01905
<i>Guaiacum sanctum</i> L.	Zygophyllaceae		Chase et al., 1993	

§ Publication in which an *rbcL* sequence for this taxon was first cited.

Abbreviations used: Arb., arboretum; BG, botanical garden; G, garden; Natl., national; RBG, Royal Botanic Gardens; Trop., tropical; U, university; herbarium acronyms are the standard ones.

## STATISTICAL SUMMARY OF SOME OF THE ACTIVITIES IN THE MISSOURI BOTANICAL GARDEN HERBARIUM, 1997

	Vascular	Bryophyte	Total
<b>Acquisition of Specimens</b>			
Staff Collections	20,611	6,523	27,134
Purchase	18,330	3,065	21,395
Exchange	29,942	3,992	33,934
Gifts	<u>11,830</u>	<u>1,169</u>	<u>12,999</u>
Total acquisitions	80,713	14,749	95,462
<b>Mountings</b>			
Newly mounted	49,706	12,095	61,801
Mounted when received	<u>18,234*</u>	<u>0</u>	<u>18,234</u>
Total specimens filed	67,940	12,095	80,035
<b>Repairs</b>			
Specimens repaired	27,241	n/a	27,241
Specimens stamped	<u>1,881</u>	<u>n/a</u>	<u>1,881</u>
Total repairs	29,122	n/a	29,122
<b>Specimens sent</b>			
On exchange	49,071	312	49,383
As gifts	<u>15,560</u>	<u>1,075</u>	<u>16,635</u>
Total	64,631	1,387	66,018
<b>Loans sent</b>			
Total transactions	410	27	437
Total specimens	32,846	4,586	37,432
To U.S. institutions			
Transactions	256	18	274
Specimens	22,374	2,856	25,230
To foreign institutions			
Transactions	154	9	163
Specimens	10,472	1,730	12,202
To student investigators			
Transactions	59	4	63
Specimens	10,160	509	10,669
To professional investigators			
Transactions	326	23	349
Specimens	22,553	4,077	26,630
<b>Loans received</b>			
Transactions	319	20	339
Specimens	33,697	2,204	35,901

\* The 18,234 "mounted when received" vascular plants are specimens of Chinese plants purchased directly from China.

	From U.S.A.	From abroad	Total
Visitors	342	107	449

On 31 December 1997 the total number of mounted, accessioned specimens in the herbarium was 4,777,217 (4,482,859 vascular plants and 294,358 bryophytes).

The Garden's herbarium is closely associated with its database management system, TROPICOS. For example, many of the numbers in the preceding chart are taken from TROPICOS, since it is used as a herbarium management tool. Herbarium labels for newly collected specimens are generated through TROPICOS, and the information is retained there for further use. The charts below summarize some of the statistics from TROPICOS both for the calendar year 1997 and as year-end totals. Note that the specimen records in TROPICOS are primarily based on MO specimens, meaning that about seventeen percent of the bryophytes and twenty-six percent of the vascular plants in the herbarium are now computerized, with an overall total of about twenty-six percent. Distributional records are taken both from herbarium specimens and from literature records, and these are distinguished in TROPICOS. Similarly, information concerning types is taken both from the literature (protologues) and from specimens.

TROPICOS is essentially complete for the names of mosses, except forms, and contains a few thousand records for hepatics, for which no comprehensive effort has yet been undertaken. The 1997 additions to the names for bryophytes, 504, reflects pretty accurately the number of nova published for that group.

TROPICOS records—1997 additions

	Bryophytes	Vascular Plants	Total
Specimens	7,685	92,778	100,463
Names	504	24,545	25,049
Synonyms	944	15,725	16,669
Distributions	1,869	22,545	24,414
Types	123	16,475	16,598
Bibliography	1,348	2,399	3,747

TROPICOS records—Year-End 1997 Totals

	Bryophytes	Vascular Plants	Total
Specimens	50,338	1,179,217	1,229,555
Names	93,121	697,741	790,862
Synonyms	57,614	335,957	393,571
Distributions	36,330	692,513	728,843
Types	6,671	208,981	215,652
Bibliography	18,284	53,178	71,462
Specimens in herbarium	294,358	4,482,859	4,777,217
Percent computerized	17	26	26

—Marshall R. Crosby